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SOME ASPECTS OF THE LIFE HISTORY AND BEHAVIORAL ECOLOGY OF THE REDLIP BLENNY (*OPHIOBLENNIUS ATLANTICUS*) (PISCES: BLENNIIDAE)

by

(C) CHRISTOPHER HOWARD MARRARO

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Some Aspects of the Life History and Behavioral Ecology of the Redlip blenny (*Ophioblennius atlanticus*) (Pisces: Blenniidae)" submitted by Christopher Howard Marraro in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

April 21, 1978.

ABSTRACT

The Redlip blenny, *Ophioblennius atlanticus*, is a common, shallow-water Caribbean reef fish. Adults of both sexes hold permanent territories. The sex ratio of the species was empirically determined to be 1:1. Although blennies defend their territories against intraspecific and interspecific competitors, blennies do share the substrate and the resources within that area with guild members. Data indicate that Redlip blennies utilize an acute topographical memory in maintaining territorial boundaries. Evidence is presented to suggest that resident Redlip blennies which become displaced from their territories are highly susceptible to predation and probably do not survive. Territoriality in Redlip blennies is requisite for reproductive activities which include: spawning, maintenance of a nest site, and care and defense of demersal eggs. The male selects and prepares a nest within his territory. Demersal eggs are maintained and cared for by the male until hatching occurs. During the early morning hours (0600-0845 hrs.) mature females leave their territories and search for nesting males. Female reproductive behaviors include: recognition of a nesting male, spawning, and homing. Males are polygamous: several females were seen breeding with a single male. The repertoire of courtship behaviors is described. Although reproduction in the species is a year-round phenomenon, a peak in reproductive activity is recognized during February and March. Reproductive periodicity in Redlip blennies is correlated with the full moon phase of the lunar cycle.

Fecundity increases exponentially with length, and this relationship for *O. atlanticus* is defined by the equation:

$$F = 7.65 \times 10^{-4} L^{3.449} .$$

A description of the eggs and early larval period is reported. The early larval period is easily identified by reference to the characteristic melanophore pattern on the ventral area. The incubation period was determined to be 84-96 hours at 29°C.

Recruitment appears to be the result of settlement by large unmetamorphosed pelagic larvae which are two to three months old. The pelagic larvae enter the adult habitat and undergo metamorphosis within the substrate. After metamorphosis, they appear on the reef as juveniles and form "interstitial" territories. Although recruitment is a year-round phenomenon, a seasonal peak (early mid-summer) is hypothesized.

Beyond metamorphosis, growth is isometric with respect to length: weight. The functional relationship between length and weight for the combined male and female data is defined by the equation:

$$W = 3.5 \times 10^{-6} L^{3.27} .$$

Age was estimated by plotting the frequency of the ratio of weight:length. Two modal peaks are hypothesized. The growth rate appears to be quite high (5-6 mm/month) during the first year, and then is drastically reduced (< 1 mm/month) for the remainder of the individual's life span. Theoretical growth for the combined male and female data is defined by the von Bertalanffy growth equation:

$$L_t = 84.81\ (1-e^{\ 1.8293(t+0.0201)}) \quad .$$

The present study attempts to describe the factors that determine reef fish community structure through the examination of the biology of the Redlip blenny. The conclusion is that blennies are not precise habitat specialists and that they are adapting to the unpredictability of living space within their environment. The life strategy of Redlip blennies is best illustrated by the unpredictability hypothesis which may also explain the maintenance of within-habitat diversity of coral reef fish.

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CHAPTER I

INTRODUCTION

The coral reef fish community is a complex biological system which is characterized by a highly diverse assemblage of species. Although the maintenance of such high diversity has been a focal point of investigation (Smith and Tyler 1972, Russell *et al.* 1974, Goldman and Talbot 1975, Sale and Dybdahl 1975, Smith and Tyler 1975), Sale and Dybdahl (1975) emphasized that "a fuller understanding of community structure will urgently require far greater information than we now have concerning reproductive seasons, fecundity, larval behavior, and growth of reef fishes."

The purpose of this investigation is to examine the biology of the Redlip blenny, *Ophioblennius atlanticus macclurei*, as a unit in the community of reef fish. The present study attempts to describe the factors that determine reef fish community structure through the examination of the biology of a common, shallow-water, primary consumer. The life history strategy of *O. atlanticus* has been examined during this investigation. The topics which are discussed include: spawning seasonality and periodicity, reproductive behavior, fecundity analysis, ontogeny, recruitment, and age and growth. In addition, the strength of territoriality in Redlip blennies was tested during the investigation, and the results are discussed. Observations on interspecific social behavior are also reported.

Springer (1962) reviewed the genus *Ophioblennius*, and described the morphology of the Redlip blenny, *O. atlanticus macclurei*. Adult

Redlip blennies range in size from about 58 mm to over 90 mm TL. Coloration is characterized by a predominantly dark chocolate-brown body, with red lips, reddish translucent pectoral fins, and a reddish trim extending around the edge of the caudal fin and onto the posterior regions of the dorsal and anal fins. Nursall (1977a) described color change and color variability in Redlip blennies. Individuals possess a group of branched cirri on the margin of the anterior nostril and unbranched cirri on the nape. The functional significance of these cirri is not known, although Able (Gibson 1969) noted that the cirri of *Blennius inequalis* serve as releasers for the female during courtship. Redlip blennies exhibit sexual dimorphism; there are strong differences between the urinogenital papillae of males and females.

Ophioblennius atlanticus macclurei is widespread in the Caribbean Atlantic (Springer 1962). Redlip blennies inhabit the shallow-water surge zone and live on solid substrate that consists of live coral and coralline rock. Adults hold permanent territories; Nursall (1977a) described in detail territoriality in Redlip blennies. Redlip blennies have demersal eggs, and the male defends the nest and cares for the eggs (Bohlke and Chaplin 1968). Redlip blennies are herbivores, and forage on filamentous algae which grow on the hard substratum (Randall 1967).

The studies reported in this paper took place along the St. James Coast, Barbados. The study period was May 1976 through March 1977. Because of an injury sustained by the author, field data for some areas of the investigation are not available for the period November 15, 1976 through January 25, 1977.

CHAPTER II

DESCRIPTION OF THE STUDY SITE

Barbados is a relatively small coral island (430 km^2) which lies 145 km to the east of the Lesser Antilles (59°37'W; 13°4'N). The surface sea temperature around Barbados ranges from a mean low of 26.8°C during February, March, and April to a mean high of 28.5°C during the months July through September (Lewis and Fish 1969). The tidal rhythm is semidiurnal. Lewis (1960) estimated the mean tidal amplitude at 70.0 cm and the tidal range at 110.0 cm.

The studies reported here took place on the south fringing reef adjacent to the Bellairs Research Institute, St. James, Barbados (Fig. 2-1). The south fringing reef is approximately 250 m long and 150 m wide. The depth varies between one and eight meters (Fig. 2-2).

Lewis (1960) described the topography and coral communities along the St. James Coast of Barbados. Lewis recognized three zones of inshore fringing reefs: Reef Flat Zone, Reef Crest Zone, and the Seaward Slope.

The Reef Flat Zone is a wide area (10-70 m) of flat reef rock that lies between the shore and the area of actively growing coral.

The Reef Crest Zone is the climax zone of the living reef. The basic features of this zone include spurs or ridges which project outward toward the sea. Irregular winding valleys run between the ridges. The spurs lie perpendicular to the shore and have an irregular outline. The surface of the zone is characterized by dead coral rock which is secondarily encrusted with *Porites porites* and *P. astreoides*.

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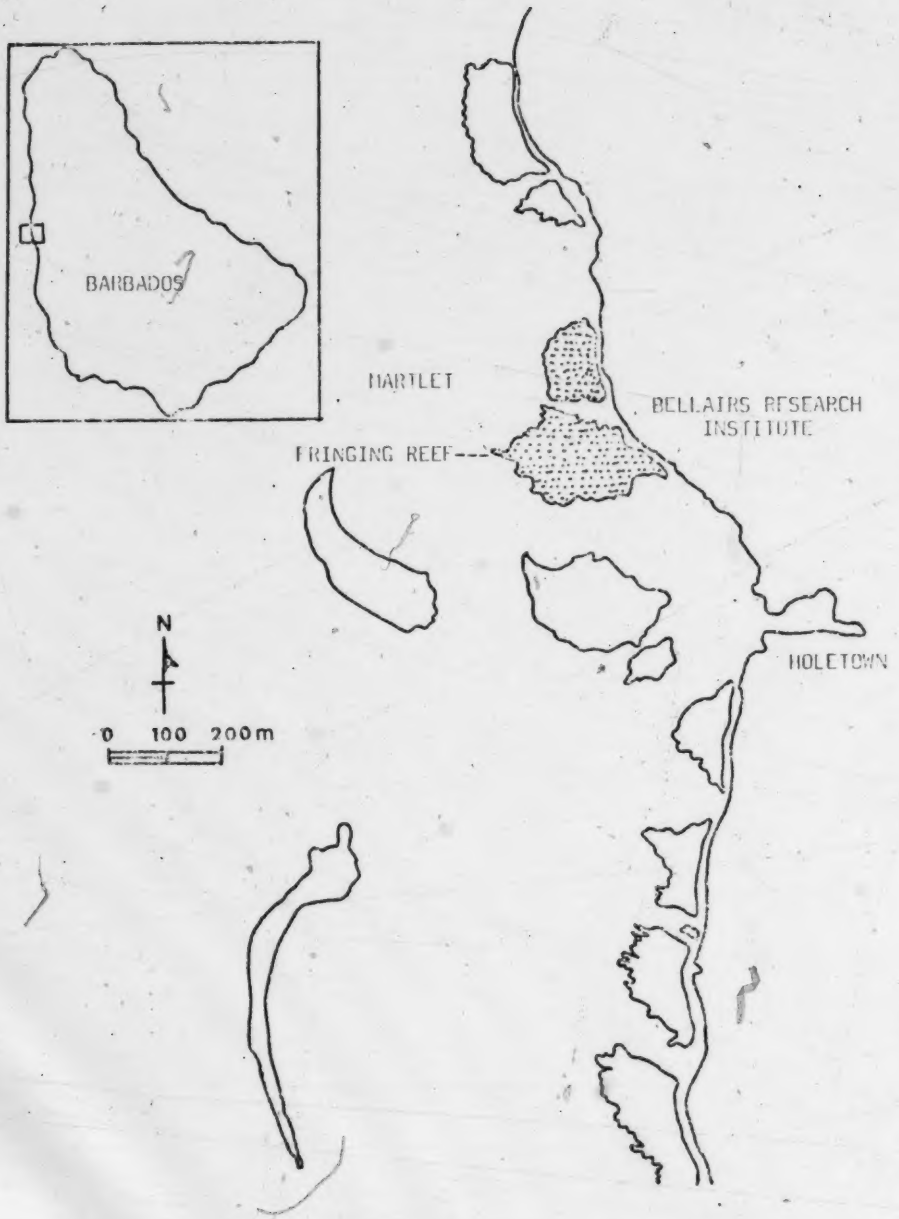
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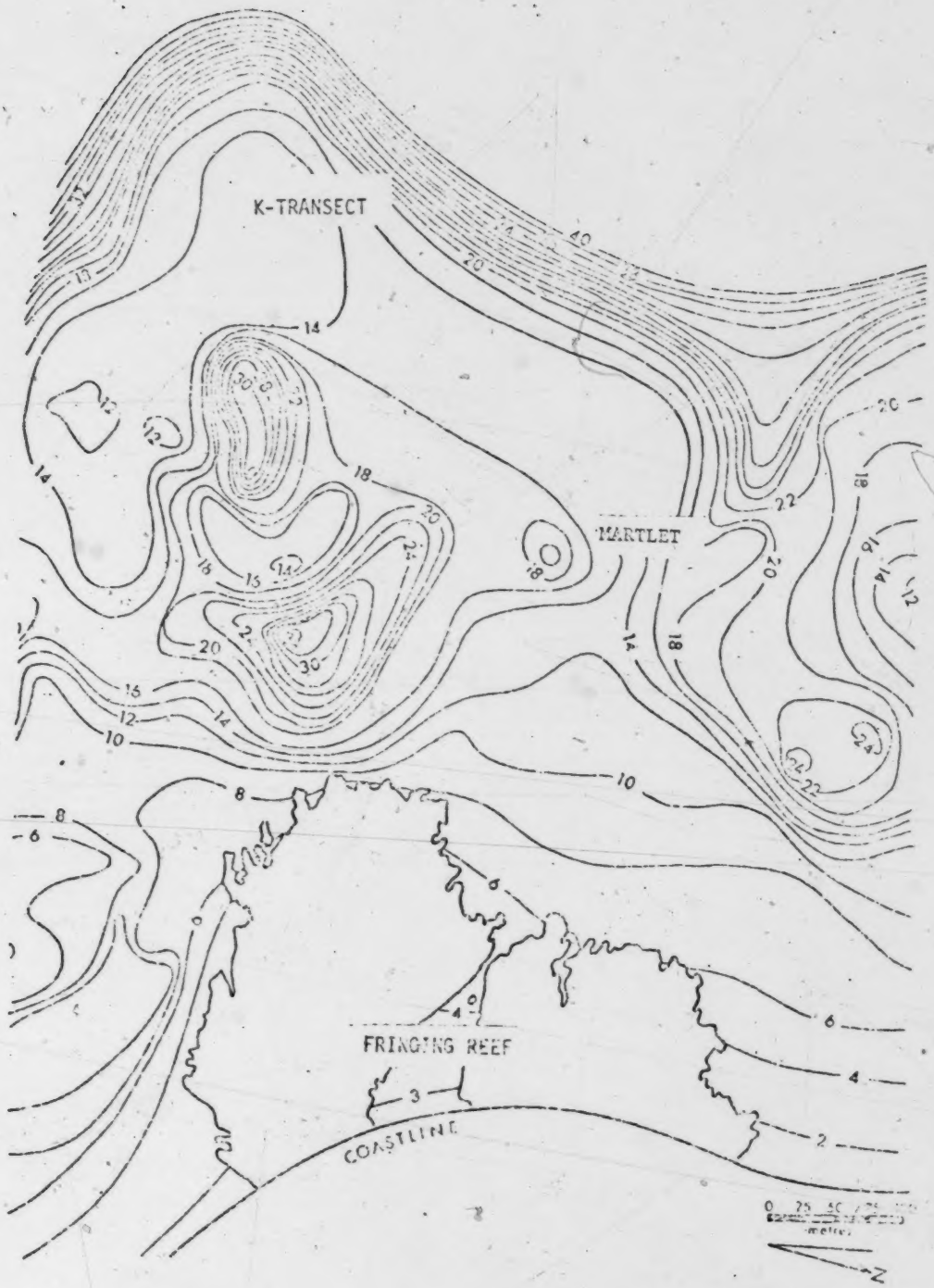
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COASTLINE

The dominant corals and chief structural elements of this zone are *Montastrea annularis* and *Siderastrea siderea*. Other corals which are abundant in this zone are *Millepora* sp. and *Montastrea cavernosa*. Most of the field observations and experiments which are reported in this paper took place on the Reef Crest Zone where *O. atlanticus* is most abundant.

At the outer limit of the Reef Crest Zone massive boulders which are separated by sand valleys appear. These ridges and valleys are continuous with the Reef Crest Zone. This area is characterized by a gradual slope of the reef to a depth of six to eight meters and is termed the Seaward Slope. The outer limit of the Seaward Slope is represented by low ridges which appear as outcrops (1-3 m high) from a sand bottom. The valleys are less regular and tend to divide and form large open sand patches. The dominant coral of the Seaward Slope is *Montastrea annularis*.

The Redlip blenny is primarily a shallow-water species which is most commonly found living on coralline rock in the Reef Crest Zone. Redlip blennies do inhabit the inner areas of the Seaward Slope, but are only infrequently observed at the outer limits of the Seaward Slope where the reef descends to a depth of six to eight meters.

CHAPTER III

METHODS

Field observations were conducted using a snorkel and mask in depths from one to three meters. Redlip blennies do not appear to be disturbed by the presence of a floating observer provided that there are no violent movements or too close an approach. Redlip blennies inhabit the surge zone and probably consider the observer to be part of the environment. Field observations and experimentation which were carried out in slightly greater depths (4-6 m) required the use of SCUBA. Observations were recorded with a pencil on a hard plastic slate. Direct observation totaled approximately 400 hours.

Redlip blennies were collected using several methods. Most individuals were removed by means of a steel spear which was powered by a finger-held elastic band. Several individuals (2-4) were collected each week for gonad analysis. These blennies were speared at random along a 40 m and a 100 m transect line which ran perpendicular to each other on the south fringing reef adjacent to the Bellairs Institute. The position along the transect lines where a blenny was to be removed was chosen using a random numbers table.

Redlip blennies which were used in field experiments were removed from marked territories through the use of rotenone ("Chemfish"), which was applied to a small area with a laboratory squeeze bottle. Blennies which were affected by rotenone treatment usually swam into a crevice within their territory. A slurp gun was used to facilitate capture of these individuals. The blennies were allowed to recover

in a perforated holding container which was placed on the reef. A fish quickly placed in water without rotenone will recover rapidly and be unimpaired.

Redlip blennies exhibit sexual dimorphism; there are strong differences between the urinogenital papillae of males and females. The sex of these captured blennies was determined *in situ*, using a hand-held lens. This procedure was carried out underwater.

Redlip blenny larvae were collected over the south fringing reef at night in surface tows. The sampling gear consisted of a half-meter (#6 mesh) plankton net. The net was towed behind a two-meter boat powered by a 5 h.p. engine. During sampling, the boat was headed into the current, the engine was set at one speed, and the net was fished for 10 minutes. Redlip blenny larvae taken in these tows were identified in the laboratory through a comparison with larvae which had hatched in the laboratory from Redlip blenny eggs collected in the field.

The method used to map territorial boundaries was described by Nursall (1977a). The boundary limits of a territory were defined by placing colored markers at points visited and vacated by a blenny as it patrolled its territory. A territory can be accurately mapped within a half-hour. Resident Redlip blennies ignored such markers and were not disturbed by their presence.

The activity patterns of males in reproductive condition were examined in detail by reference to a 1 m^2 grid which was placed over the territory of the male. Males exhibited no adverse reactions to the grid.

Eggs and developing larvae were examined under a Wild M-6 dissecting microscope, and their measurements were taken with the aid of an ocular micrometer. A stage micrometer was used to calibrate the ocular micrometer.

A life history investigation requires the development of a diverse set of experimental procedures. A detailed description of the methods employed in the different parts of this investigation is reported within each section.

CHAPTER IV

REPRODUCTIVE SEASONALITY AND PERIODICITY

The phenomena of reproductive seasonality and periodicity in coral reef fishes, problems of considerable ecological importance, have not been adequately investigated. In addition, little information is available concerning the environmental factors which influence reproductive periodicity of reef fish species.

Erdman (1956) presented evidence of spawning periodicity in 34 species of reef fish from Puerto Rico. Feddern (1965) presented data on the reproductive activities of the Bluehead wrasse (*Thalassoma bifasciatum*). This species was found to spawn in the Virgin Islands during all months of the year except September. Munro *et al.* (1973) investigated reproductive activity of 83 species of reef fish from Jamaica. These authors described seasonality for 35 species. A peak in reproductive activity is recognized during the spring (February to April), although year-round spawning appears to be indicative of some families. Powles (1975) described seasonality in larval abundance of inshore reef fish families from Barbados. He concluded that there are two peaks in seasonal abundance of inshore reef fish larvae: a spring peak (March-May), and a fall peak (August-October). Luckhurst and Luckhurst (1977) investigated recruitment patterns of 16 species of coral reef fish from Curaçao. They recognized two seasonal peaks (March-May, September-November) in abundance of recruits for species examined. In addition, recruits of some species were present throughout the year, a fact which suggested that spawning is also a year-round phenomenon in these species.

Reproductive seasonality and periodicity in the Redlip blenny have been examined during this investigation. Data were collected over an 11-month period (May 1976-March 1977). In order to establish seasonality sufficiently, a minimum of two annual cycles is required. Therefore, the importance of the results of this study is reduced, since the data represent only 11 months of investigation. Nevertheless, evidence is presented to indicate that reproduction in the Redlip blenny, although seasonal, occurs throughout the year and also that reproductive periodicity is correlated with the full moon phase of the lunar cycle.

Results

Reproductive seasonality and periodicity in the Redlip blenny were determined by several methods.

Direct evidence of spawning periodicity was obtained by monitoring incidents of spawning along a transect line. Observations were made at least once a week during the months of July to mid-November and February through March. A 50-meter transect line was established on the south fringing reef adjacent to the Bellairs Institute. Lewis (1960) described the coral reef communities and topography along the St. James Coast, Barbados. Because spawning activity in the Redlip blenny is limited to the early morning hours, all observations were initiated at 0600 hours. Sampling time was approximately one hour.

Both sexes of the Redlip blenny maintain permanent territories; non-reproductive extra-territoriality is not common (Nursall 1977a). The male of the species prepares a nest cave within his territory and

is also responsible for the care and defense of the eggs (Bohlke and Chaplin 1968). These behaviors provide a basis from which a definition of an incident of spawning is formulated. The occurrence of two blennies in the same crevice is a highly improbable event unless these fish are engaged in reproductive activity. Therefore, an incident of spawning is defined as the occurrence of both male and female in the nest site for a duration of at least 10 seconds.

A further constraint placed on this method of investigation is that the population numbers of blennies must remain relatively constant over the study period. Census data were taken during August and again during February. Since both sexes are territorial, the census data are quite accurate. An estimate of 84 individuals was recorded in August, and an estimate of 79 individuals was recorded in February.

The results of the transect investigation are listed in Table 4-1 and are plotted in Figure 4-1.

These results indicate both that reproduction is occurring in all months sampled, and that the greatest number of spawning incidents in any month appears to coincide with the full moon phase of the lunar cycle. A correlation between moon phase (defined as full moon or new moon) and spawning activity was tested using Spearman's Rank Correlation Test. A significant value ($P < .05$) for $r = .92$ was obtained. The higher number of spawning incidents observed in August, September, October, and March as compared with July and February may not be used to infer seasonality. These data may not indicate spawning intensity because it is quite possible that fewer incidents of spawning were reported than had occurred. Also, the lower peak of spawning activity

TABLE 4-1. Incidents of spawning along a 50 m transect line.

Sample Date	Incidents of Spawning Along 50 m Transect Line	Moon Phase
7/07/76	4	FQ
7/13/76	20	Full
7/26/76	0	New
8/01/76	0	FQ
8/09/76	40	Full
8/16/76	4	LQ
8/25/76	0	New
8/30/76	1	FQ
9/01/76	3	FQ
9/07/76	32	Full
9/10/76	35	Full
9/17/76	0	LQ
9/24/76	0	New
10/01/76	0	FQ
10/05/76	26	Full
10/08/76	35	Full
10/12/76	31	Full-LQ
10/18/76	5	LQ
10/25/76	0	New
11/01/76	1	FQ
11/07/76	24	Full
11/13/76	4	LQ
1/30/77	4	FQ
2/01/77	12	Full
2/07/77	8	Full-LQ
2/14/77	0	LQ
2/18/77	0	New
2/25/77	3	FQ
2/28/77	3	FQ
3/07/77	31	Full
3/15/77	1	LQ-New
3/23/77	0	New-FQ

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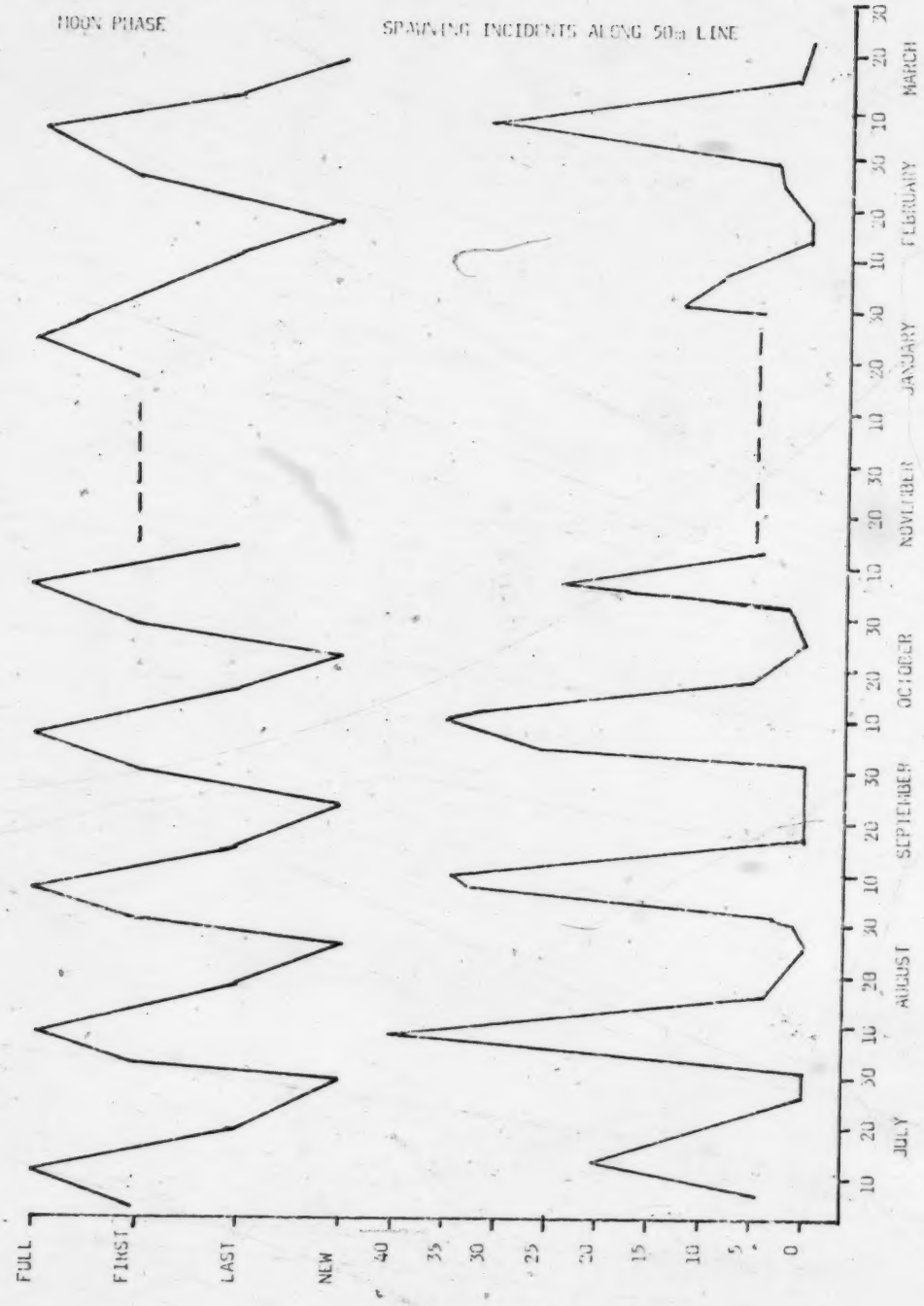
MOON PHASE
SPAWNING INCIDENTS ALONG 50m LINE
FULL
FIRST
LAST
NEW
40
35
30
25
20
15
10
5
0
10 20 30
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
JANUARY
FEBRUARY
MARCH

seen in February may not be significant because observations were made a full three days before full moon. No observations were made at or just after the full moon phase during February.

Egg collections provide further evidence of reproductive periodicity. Egg masses were collected on the south fringing reef during the months of May-November 1976 and January-March 1977. No diving was undertaken from mid-November to December 1976, so no attempt was made to collect egg masses then. No quantitative data are available for these collections, because only small irregular samples were taken for the purpose of ontogenetic examination. Nevertheless, the fact that egg masses could be collected in all months sampled indicates that spawning is a year-round phenomenon.

Spawning seasonality was determined by monitoring the mean monthly changes in the gonadosomatic index for males and females. Each week of the sample period, three to seven adults were speared at random. The gonads were removed in the laboratory, and weighed to ± 0.001 grams. The body weight (less gonad weight) was also recorded to ± 0.001 grams. The ratio of gonad weight to body weight (GSI) was then calculated for each fish.

The range, means, and 95% confidence limits of this ratio were estimated for males and females. These parameters are plotted for each month (Figs. 4-2, 4-3). In addition, the range low and mean GSI ratio of eight other known spawning females and 11 other known spawning males are plotted on the same graph.

The general shape of the curve as well as the fact that there is a significant increase in female gonad:body weight (t-test, $P < .05$)

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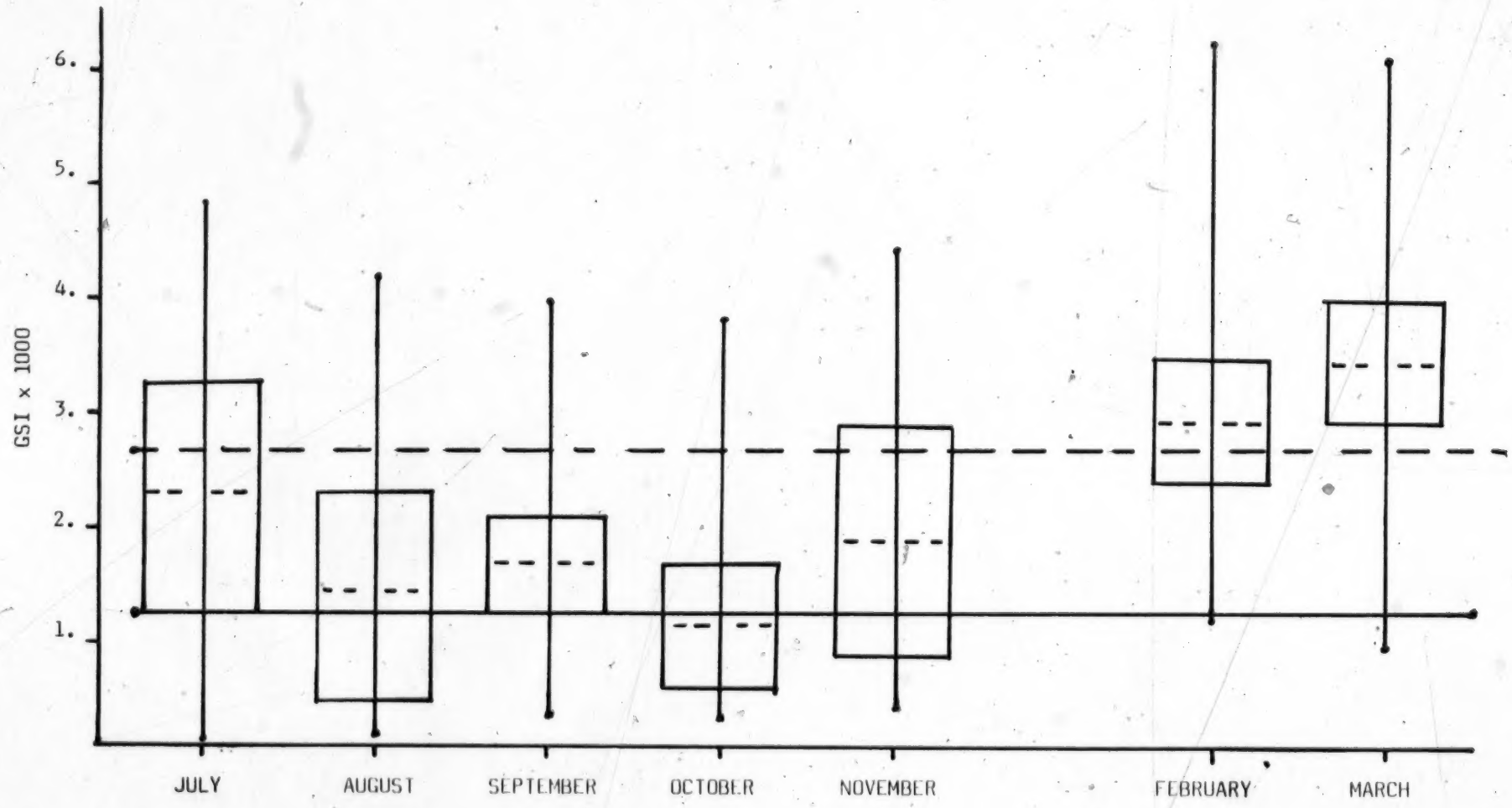
GSI x 1000
6.
5.
4.
3.
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JULY
AUGUST
SEPTEMBER
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NOVEMBER
FEBRUARY
MARCH

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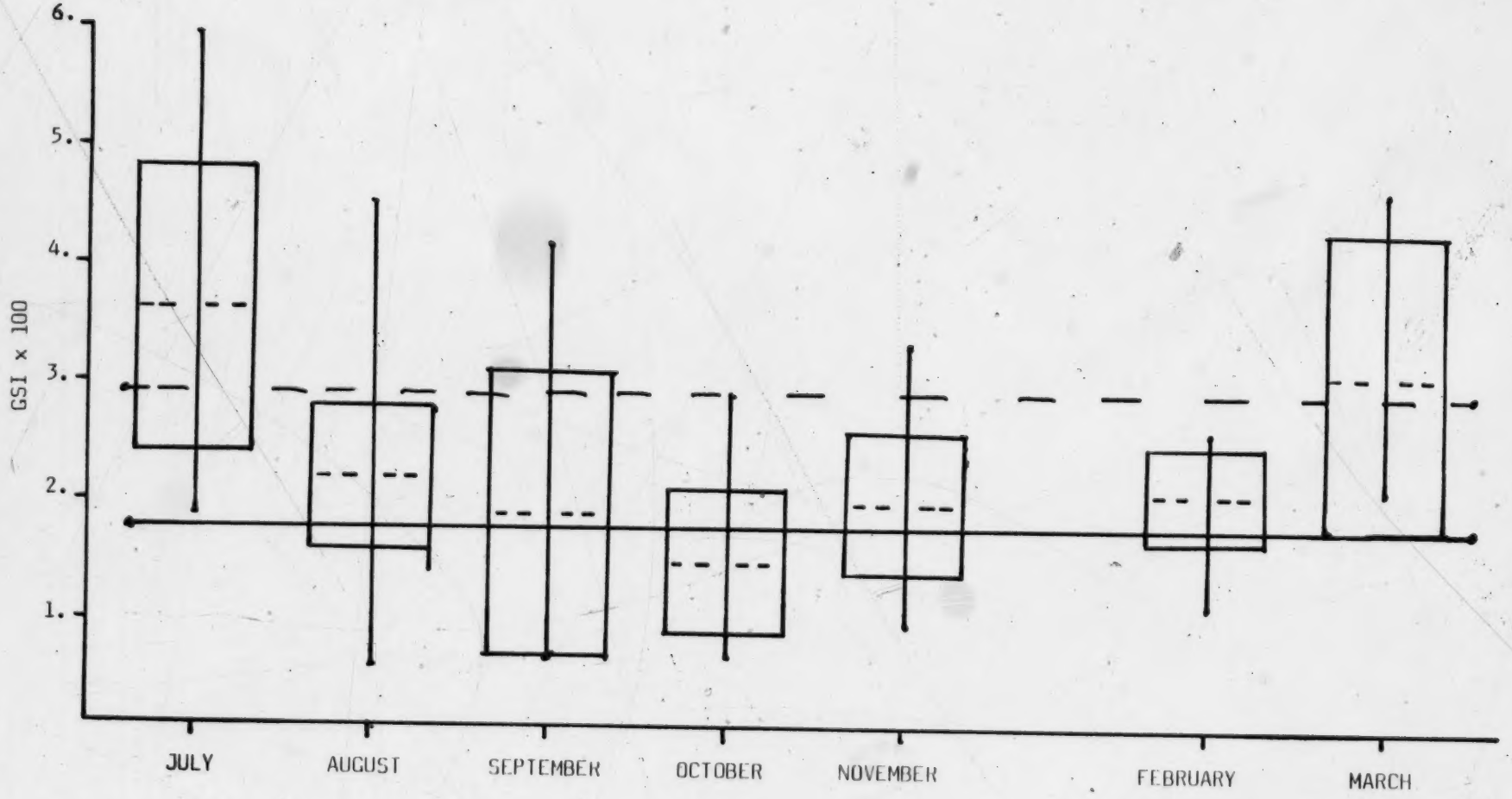
6.
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GSI x 100
JULY
AUGUST
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FEBRUARY
MARCH

between October and February appears to indicate that spawning activity occurred during February and March. Although sample sizes for males are too low to calculate significance, the data appear to follow the same general trend as those for females. A modified interpretation may be made when the range and confidence limits of the GSI ratios are examined and compared with the range low and mean GSI ratio of the known breeding individuals. The results now indicate that although a greater proportion of the population appears to be spawning during February and March, breeding does occur during the other months sampled. These results support previous investigations (Munro *et al.* 1973, Powles 1975) cited earlier in this section.

Finally, an analysis of larval catch rates was employed to determine reproductive periodicity in the Redlip blenny. The sample period was mid-July to August, inclusive, and October 1976 through March 1977. Weekly surface tows were taken over the inshore fringing reef adjacent to the Bellairs Institute. Inshore tows were chosen because Powles (1975) had determined that the larvae of most inshore reef fish families are found in greater numbers in inshore surface tows than are found in offshore step-oblique tows. All tows were taken over a standard course. No blenny larvae had been caught previously in 18 daylight tows. Therefore, all tows during the sample period were taken at night (1900-2200 hrs.). Sampling gear consisted of a 0.5 meter (#6 mesh) plankton net. The net was supplied with a TSK flowmeter. The flowmeter was calibrated by towing the net between two marker buoys which were a known distance apart (Jake Kafri, personal communication). Flowmeter data exhibited considerable

variability in the amount of water filtered per tow, around a mean value of 115 ± 2.5 m^3 water/tow. The extreme range for these tows is 99-141 m^3 water/tow. The net was towed with a two-meter boat powered by a 5 h.p. engine. During sampling, the boat was headed into the current, the engine was set at one speed, and the net was fished for 10 minutes. Tide and moonphase data were recorded. The plankton net was washed down thoroughly after each use. The concentrated samples were taken to the laboratory where the fish larvae were sorted, identified, and then fixed in 5% neutral formalin.

A record of blenny larval catch rates was maintained. A capture index (catch/unit effort) was estimated for blenny larvae. Catch/unit effort (Ci) is defined as:

$$Ci = \frac{ci^{x}E}{ei^{x}C} \times 100 \text{ (Johnson and Koo 1975)}$$

where:

E = total number of samples

C = total number of blenny larvae captured

ei = number of samples taken on i^{th} day = 1

ci = number of blenny larvae taken on i^{th} day.

The results are plotted in Figure 4-4.

High capture indices are recognized during the months of August, November, February and March. Low indices were reported for December and January. Larval catch rates are highly influenced by plankton patchiness. Therefore, these results can only be defined in terms of reproductive periodicity and cannot be used to determine reproductive seasonality.

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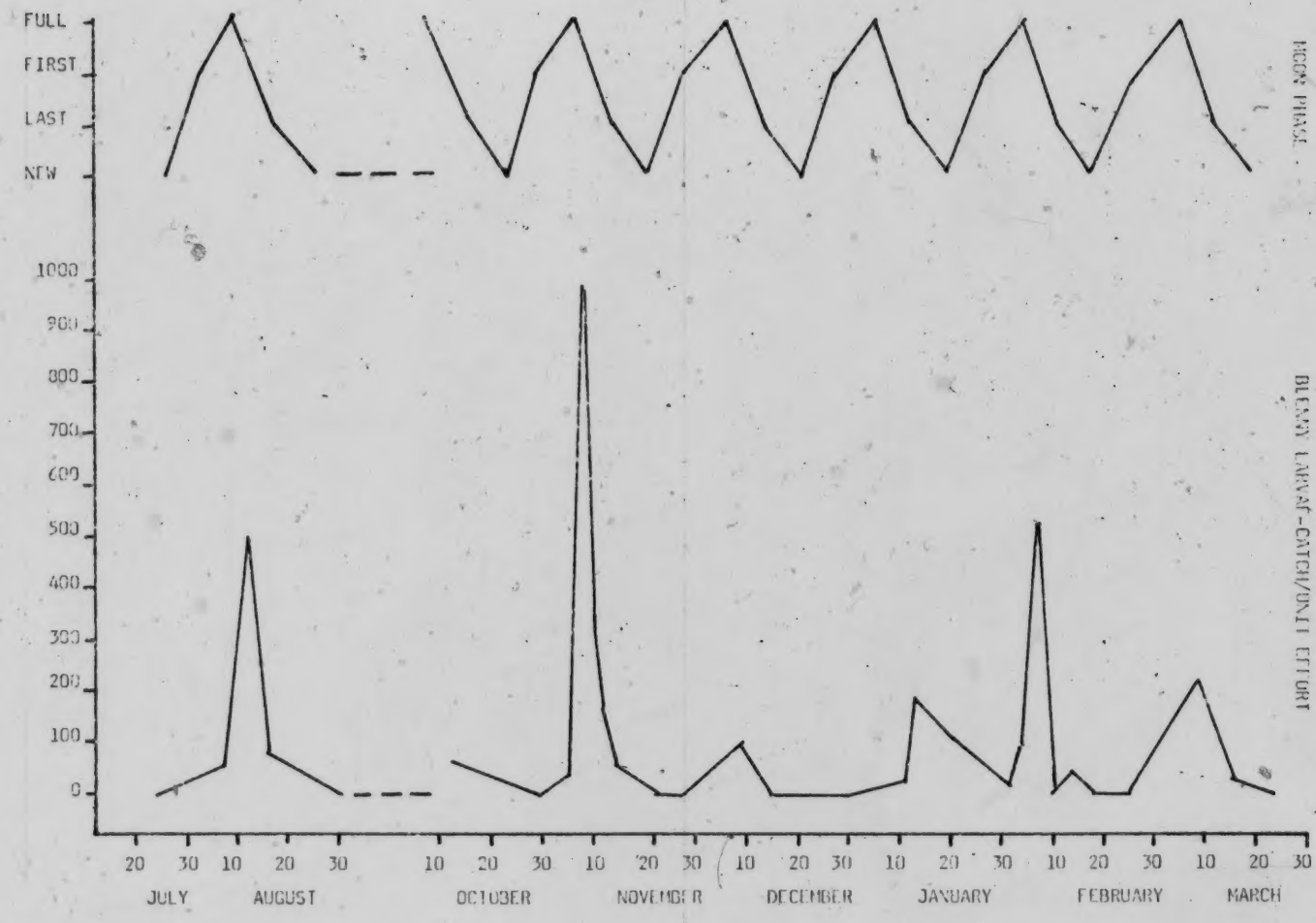

FULL
FIRST
LAST
NEW
MOON PHASE
1000
900
800
700
600
500
400
300
200
100
0
BLUEFIN LARVAE-CATCH/UNIT EFFORT
20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
JULY
AUGUST
OCTOBER
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH

The appearance of blenny larvae in the plankton appears to coincide with the full moon period of the lunar cycle. Large numbers of blenny larvae appear in the plankton four days after the onset of full moon ($\overline{X}$ = 96 ± 14.8 hrs.) for each month sampled. This fact is of considerable importance, because hatching was determined to occur 84-96 hours after spawning takes place (see Chapter VII). Some blenny larvae are found in the plankton as early as the onset of the first quarter of the lunar cycle. Some spawning activity does occur between the first quarter and the full moon phases of the lunar cycle but in general, reproductive activity is concentrated at the time of full moon.

Discussion

The results discussed in this section indicate that Redlip blennies probably breed throughout the year. Evidence of reproductive activity was obtained throughout the sample period (May 1976-March 1977). In addition, reproduction in this species appears to be seasonal. The occurrence of a fall peak is not clear. More data are required to define the presence of a fall peak. The occurrence of a spring peak (February-March) is supported by data collected through GSI analysis. This seasonal pattern corresponds closely to breeding rhythms observed by Munro *et al.* (1973). These investigators found that gonad activity in reef fish from Jamaica was maximal during the period February-April, although breeding in some families did occur throughout the year. Watson and Leis (1974) described larval abundance of four species of blennies from Hawaii. Four species

appeared each to have one seasonal reproductive peak although breeding occurred throughout the year in all. The occurrence of a seasonal peak in spawning activity has been demonstrated for other species at Barbados. Lewis *et al.* (1962) investigated breeding activity in the flying fish (*Hirundichthys affinis*) and concluded that spawning takes place between January and May. Larval catches of brachyurans off Barbados exhibit spring and fall peaks, and these peaks correspond to high reproductive activity in the adults (Lewis and Fish 1969).

Luckhurst (personal communication) has suggested that periods of high reproductive activity in coral reef fish from Curaçao may be correlated with minimum water temperatures. Minimum surface sea temperatures around Barbados occur from January till March (Lewis and Fish 1969). This period of minimum sea temperature coincides with high reproductive activity (high GSI) in the Redlip blenny.

The high correlation between the occurrence of full moon and spawning activity, as well as the appearance of large numbers of blenny larvae in the plankton several days after full moon, indicates that the underlying cause of breeding periodicity in the Redlip blenny is related to the lunar cycle.

Pannella (1975) investigated otolith growth patterns in several species of tropical reef fish from Puerto Rico. He suggested that the hyaline and opaque bands of otoliths of tropical fish are related to reproductive activities and not to seasonal changes. He noted that the rings appear in multiples of months, supporting the idea of lunar influence on the reproductive cycles of certain tropical fish. Lunar influence on spawning activity has been demonstrated for other species

of marine fish. Savage and Hodgson (1934) described one example. The herring fishery off the east coast of England shows maximum catches at the periods of full moon in October and November. The California grunion (*Leuresthes tenuis*) comes inshore to spawn from March to August on the three nights following full moon (Walker 1952). Walker (Gibson 1969) investigated the spawning habits of another California grunion (*Hubbsiella sardinia*), and concluded that spawning activity is associated with some factor related to the second preceding full or new moon.

The ultimate factors responsible for the lunar spawning rhythm in the Redlip blenny are not clear. Responses by the fish to tidal rhythms or to a particular threshold of illumination would seem to be the two most obvious factors.

CHAPTER V

REPRODUCTIVE ACTIVITIES

Definitions

Male in reproductive condition - a mature male (high GSI) which maintains a nest.

Breeding male - a male in reproductive condition which will accept a female into the nest in order to spawn.

Breeding period - the period of the month in which a male in reproductive condition will accept females into the nest. This period coincides with the first quarter/full moon phase of the lunar cycle.

Non-breeding period - the period of the month in which a male in reproductive condition will not accept a female into the nest. This period coincides with the new moon phase of the lunar cycle.

The reproductive activities of *Ophioblennius atlanticus* parallel patterns of reproduction described for other blennies (Fishelson 1963, Breder and Rosen 1966, Gibson 1969, Dayneko 1975, Fishelson 1975). Reproductive activities are carried out within the territory of the male. Adhesive eggs are deposited within a nest cave which has been prepared by the male. The eggs are maintained by the male until hatching occurs. This type of reproduction requires the development of specific male and female behaviors. Male behavior includes: nest preparation, attraction of females to the nest, and care and defense of the nest against interspecific and intraspecific competitors. Female behavior includes: recognition of a nesting male, spawning,

and leaving the nest. Because females hold permanent territories, they must also develop the ability to home as well as the ability to communicate to nesting males that they are reproductively active females.

Nest Selection and Preparation

A male will select a small defensible area as a nest within its territory. Typically the nest has two entrances and is located within a small crevice (≃ 5 cm wide) in the reef. However, males may also select either the underside of a solitary flat rock or even live coral as a nest. Nests have been found within a hollowed portion of *Montastrea annularis*, or among the branches of finger coral (*Porites porites*). One nest site was located within the base of a hollowed section of fire coral (*Millepora* sp.). Egg masses are deposited on the walls and ceiling of the nest.

Nest sites can be identified by the position and behavior of the resident in his territory. Redlip blennies are diurnal, and are normally quite active on their territories (Nursall 1977a). Nest guards, however, limit their activities to the nest area and only infrequently leave the nest. Typically a nest guard is seen with only his head or the anterior part of his body to the pelvic fins protruding. Feeding activity by nest guards during the early morning hours (0600-0900 hrs.) is not common. During the afternoon period, the nest guard periodically leaves the nest for 5-15 seconds in order to feed at favored areas within the territory and then darts back to the nest.

Nest preparation activity by the male is not frequently observed, but several incidents were seen during the investigation. In two of these instances, males were seen removing debris from crevices and depositing this debris at the perimeter of their territories. The debris consisted of sand and pieces of coralline rock. The activity persisted for several seconds in one case and for over a minute in the other instance. Spawning activity was observed in both these crevices several days later. In addition, nest guards were observed frantically removing debris when nest sites had been destroyed in order to obtain egg samples. Colored markers were sometimes used to mark the position of active nests. In most cases, the males would move these markers away from the nest to the perimeter of the territory. This distance varied from about 5 to 30 centimeters.

Female Pre-spawning Activities

Spawning activity is limited to the early morning hours. The time of spawning was monitored at seven nest sites for a one-week period during March. Spawning was observed to occur during the first three hours of daylight. During the entire investigation (June-March), no spawning incidents were recorded after 0845 hrs.

Females leave their territories during this period (0600-0900 hrs.) searching for males that are in reproductive condition. The straight-line distance traveled to a spawning male's territory by a female was measured for 19 females during the investigation: = 2.39 ± 0.3 meters; range = 0.25 - 5.2 meters. The mean time that females stay within a nest was estimated to be = 16.9 ± 3.3 minutes. Females must exhibit

homing behavior and utilize an acute topographical memory in order to locate and to recognize their territories after spawning. The results of territory experiments (see Chapter X) show that Redlip blennies can easily recognize their territories and regain control from transgressors (Nursall 1977a) up to 3.5 hours of being absent from their territories. Since the spawning period represents a maximum of three hours, females are in little danger of either not recognizing their territories or of losing control of their territories to possible transgressors.

In general, breeding occurs during the full moon phase of the lunar cycle. However, some spawning incidents have been recorded as early as the onset of the first quarter phase. Although female reproductive extra-territoriality typically occurs throughout the lunar cycle, this activity appears to increase just before the first quarter phase to several days after the full moon phase. Females appear to explore and to search for breeding males or potential nest sites. In one incident (October 25, 2 days after new moon) a blenny swam 3 to 4 meters to a territory of a male that had been breeding two weeks earlier. The swimming behavior of this fish was peculiar and was characterized by quick jerky movements of the caudal fin. The fish appeared to "skip" across the substrate. Then the fish "lay across" (Nursall 1977a) the male. The "lying across" activity persisted for two minutes and then the fish moved back to its territory. The territory of this female was marked. On a subsequent visit (November 4), the fish was seen spawning with that particular male. During the second incident (February 18), a blenny "skipped" two meters and then

rested next to a male that had been nesting a week earlier. This male nudged the fish off the territory. The fish swam towards the territory of another reproductive active male. This male chased the fish off his territory. The fish finally moved back to its own territory and remained there. Both these incidents occurred during the non-breeding period.

Three to six females may aggregate at the perimeter of a nesting male's territory. Although these aggregations do occur throughout the lunar period, they are most frequently observed during the breeding period. An individual commonly will leave the aggregation and approach the nesting male. The female will usually display a form of the "S" pattern and then will be chased off the territory by the nesting male. The chasing action by the male causes the other females in the aggregation to swim together vertically in the water column for a few seconds. This movement by several females at the perimeter of the male's territory is what commonly attracts the attention of an observer.

Spawning Sequence

Spawning behavior at 16 nest sites was observed during the investigation. Direct observation totaled more than 33 hours.

The spawning sequence commences with the arrival of a female on the territory of a breeding male. Prior to the arrival of the female, the male may display in order to attract interested females to the nest. The male, dorsal and anal fins erect, will swim from the nest for a distance of about 15 cm. The male, remaining in a horizontal plane, will "quiver" close to the substrate for one or two seconds and

will then dart into the nest. This action is performed frequently until a female arrives. Typically, the male does not display and is located within the nest when a female arrives. The female will approach the nest, and the male will usually respond by leaving the nest and swimming towards the female. In the event the male does not leave the nest, the female will elevate her body to a 45° angle, head up. She will maintain her position and will "quiver". Wickler (Gibson 1969) suggests that this female action in *Blennius fluviatilis* functions to display the swollen abdomen to the male. At this point, spawning between these two individuals is contingent on the readiness of the male to breed.

If the male is ready to spawn, he will leave the nest, dorsal and anal fins erect, and will approach the female. When the male reaches the female, he will "peck" her on the head and then return to the nest. The female responds to this action by following the male to the nest. In most cases, the male will enter the nest, then emerge from it. This action is followed by the entrance of the female into the nest. The female will, on occasion, enter the nest before the male. Only one instance was observed where a female entered the nest and was not "pecked" or approached by the male. This case involved one female and two breeding males (A1, A2) that had contiguous territories. Male A1 was breeding with the female while male A2 was displaying at the opposite end of his territory. When the female had finished spawning with male A1, she swam into the nest of male A2. Male A2, upon noticing the female entering his nest, quickly swam into the nest. The female was in the nest for only 10-15 seconds. The female then left the area.

The respective male and female behaviors described here were observed at five nest sites. Fifteen females were accepted by these five males during the observation period. The results are listed in Table 5-1.

An analysis using the Kruskal-Wallis test indicates that the five males are homogenous ($P > .05$) with respect to their treatment of the 15 females. The sequence was tested using Chi Square. The number of times that behavior X (male and female) occurred as the i^{th} behavior in the sequence is not significantly different from the expected value.

Once in the nest, the female begins to lay eggs along the walls of the nest. The female is seen rubbing her abdomen up and down on the walls. Although fertilization was not actually observed, it was assumed to take place when the male frantically moved back and forth over the areas where the female had been laying eggs. The male and female may assume one of three different positions while they are in the nest together:

(i) The male and female may be head to tail with their ventral sides facing but not touching each other.

(ii) The male and female may be head to head with their ventral sides facing but not touching each other.

(iii) The male and female may be head to head with their dorsal sides facing but not touching each other.

The male clearly assumes a more aggressive role while the female is in the nest laying eggs. During this period, the male will make periodic dashes out of the nest, turn around, peck the female if her head is visible, and re-enter the nest. During egg laying, the female

TABLE 5-1. Analysis of spawning sequence: male-female interactions at five nest sites.

Nest Site	Male in Nest When Female Arrives on Territory	Female Approaches Nest	Male Swims to Female and "Pecks"	Female Follows Male to Nest	Male Enters Nest and Emerges	Female Enters Nest After Male Emerges
A	5	5	5	5	4	4
B	2	2	2	2	2	2
C	2	2	2	2	2	2
D	1	1	1	1	1	1
E	5	5	5	5	5	5

usually keeps her head just at or above the opening of the nest. In addition, the male sometimes leaves the nest to display. The male, dorsal and anal fins erect, will raise his head until his body is elevated to a 60° angle. The male, maintaining his position, will display an exaggerated "S" pattern, then will dart into the nest. The significance of this action is not known. Wickler (Gibson 1969) suggested that movements of high amplitude in blennies are performed during an aggressive state. This behavior may be a warning to conspecifics. Other females, which attempt to gain entrance to a nest while breeding activity is in progress, are immediately chased by the male. The females which are chased usually make several more attempts to approach the nest. The male always chases such female intruders.

Egg laying will persist for a period of from several seconds to 45 minutes. After spawning, the female will leave the nest and the male will begin brood care. It is not known whether or not the male physically encourages the female to leave the nest. The female will swim at least to the perimeter of the male's territory after leaving the nest. She may rest at the perimeter for a few seconds or she may continue swimming. After leaving the male's territory, she may swim to her own territory or she may attempt to spawn with another male. Males are polygamous and as many as three different females have been observed to spawn with a single male during a two-hour period. Polygamy is also evidenced by the fact that egg masses within a nest are characterized by embryos at various stages of development. The swimming pattern of a female which has left a nest resembles the characteristic swimming pattern for intruders described by Nursall

(1977a). The female swims above the substrate. The fish periodically stops to rest, but is quickly chased by conspecifics. The chasing attracts the attention of other blennies which pursue the female. Therefore, the female is forced to swim farther between rest periods until she reaches the safety of her own territory.

The male begins brood care when the female leaves the nest. The male guards the nest and fans the eggs with his pectoral fins and caudal fins. It is assumed that males remove infected eggs. This behavior has been shown to occur in other blennies (Gibson 1969, Dayneko 1975). The male guards the nest against intruders. Juvenile Bluehead wrasses (*Thalassoma bifasciatum*) were immediately chased by the male nest guard if they approached the nest. Bluehead wrasses were always noticed to feed on blenny eggs when the male guard was removed from a nest. Species which hold territories that are superimposed over the territories of the Redlip blenny are not usually chased by the nest guard if these fish approach the nest. These species which normally co-exist with the Redlip blennies include the Dusky damselfish (*Eupomacentrus dorsopunicans-diencaeus*[1]), and the Yellowtail damselfish (*Microspathodon chrysurus*).

In general, a male that is not ready to spawn will be located in the nest when the female arrives on his territory. As noted earlier, the female will approach the nest. The female will elicit one of two possible responses in the event the male does not swim out of the nest. Typically she will either display by elevating her body to a 45° angle and will "quiver", or she will attempt to enter the nest. It was noticed that desirous females sometimes have their dorsal and anal fins

extended when they try to gain entrance to a nest. It was not known if the position of the dorsal and anal fins was a significant factor in the ultimate acceptance or rejection of the female by the male. Dorsal and anal fin extension was seen in 60 of these male-female encounters. An analysis using the Mann-Whitney Statistic indicates that the position of the dorsal and anal fins of desirous females was not a significant factor ($P > .05$) in the rejection of these females for breeding by the males. The male responds to the first female action (quivering) by either moving out of the nest or by remaining in the nest. If the male swims out of the nest, he usually will display an "S" pattern. The female will respond by either swimming back to the perimeter of the male's territory or she will continue to display. If she continues to display, the male will chase her off the territory. He will then dart back to the nest. If the male remains in the nest, the female will attempt to enter the nest. The male responds immediately by nipping at her caudal area and by chasing her from the nest. The second possible response which is elicited by the female when the male does not leave the nest is that she will try to enter the nest. The male responds by chasing her from the nest.

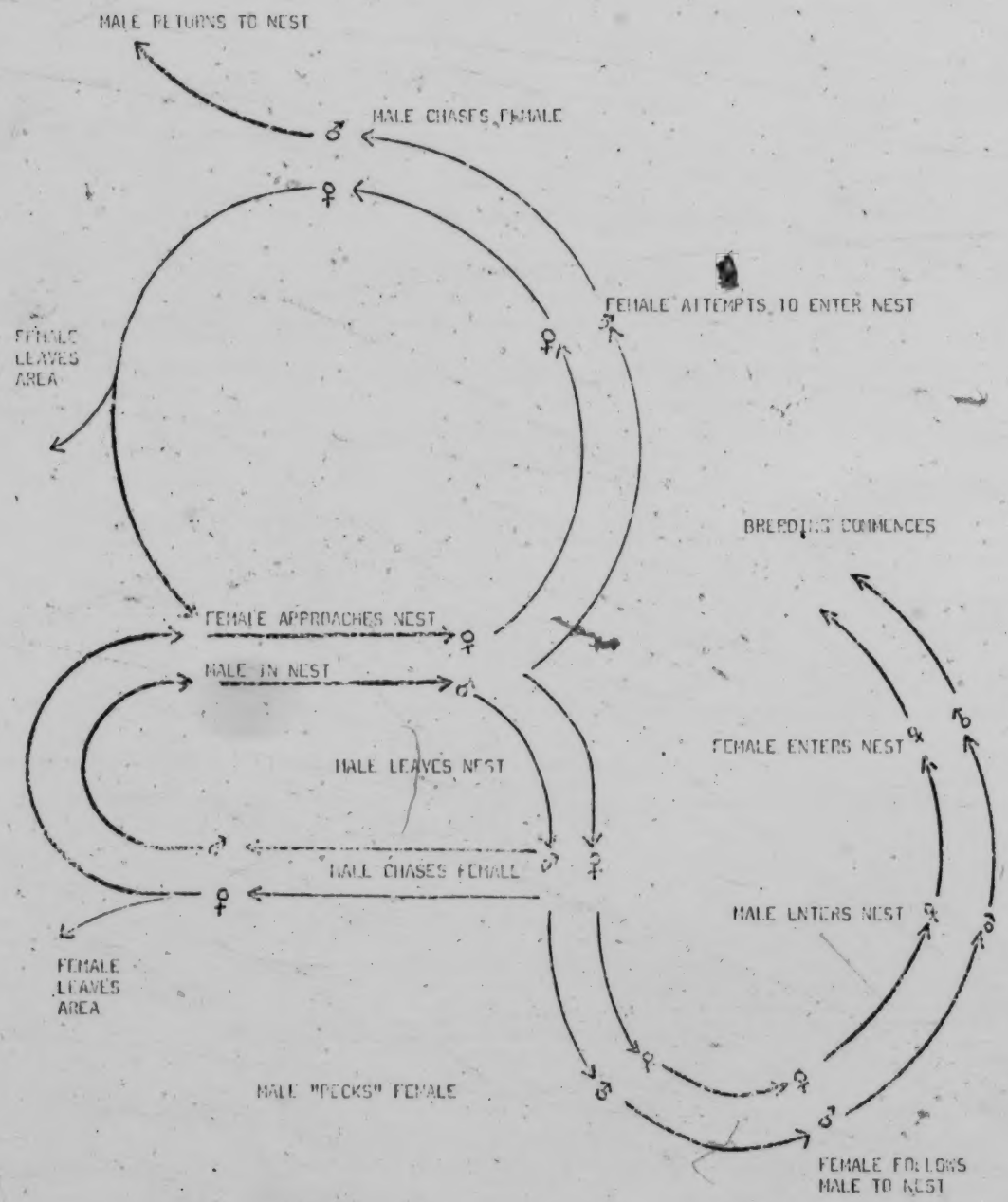
Females will approach a nest several times after they have been chased by the male. There may be several females near the perimeter of the male's territory. The greatest number of females observed at the perimeter of a breeding male's territory was six. These six females would continually approach the nest and display. Sometimes more than one female would approach the nest at a time. During one 20-minute observation period, five females approached the nest 56 times.

It was noticed that the more times the females approached the nest, the less likely the male would display and the more likely he would chase them off the territory. The repertoire of courtship behaviors is summarized in Figure 5-1.

Activity Patterns of Males in Reproductive Condition

The activity patterns of eight males in reproductive condition were examined. Specifically two parameters were considered. The first consideration was the percentage of time allocated to seven basic activities by these eight males. The activities include: feeding, moving, displaying, performing interspecific interactions, performing intraspecific interactions, resting next to the nest site, and resting within the nest. The second parameter which was considered is the percentage of time spent by these eight males in different parts of their territories.

The parameters were examined in the field by placing 1 m^2 grids which had been divided into 16 equal parts over the territories of the males. The activities of the males were recorded with a pencil on a hard plastic slate which was also divided into 16 equal squares. An effort was made to record the behavior of the fish once every 5 seconds for a 10-20 minute sample period. However, the recording time exhibited much variability around the mean value of 4.61 ± 0.2 seconds/recording for 41 sample periods. The extreme range for these recordings were: 3.13-5.78 seconds/recording. The sample periods were divided into four groups: Morning, Breeding Period; Afternoon,


MALE RETURNS TO NEST
MALE CHASES FEMALE
FEMALE ATTEMPTS TO ENTER NEST
FEMALE LEAVES AREA
BREEDING COMMENCES
FEMALE APPROACHES NEST
MALE IN NEST
FEMALE ENTERS NEST
MALE LEAVES NEST
MALE CHASES FEMALE
MALE ENTERS NEST
FEMALE LEAVES AREA
MALE "PECKS" FEMALE
FEMALE FOLLOWS MALE TO NEST

Breeding Period; Morning, Non-Breeding Period; and Afternoon, Non-Breeding Period. Morning observations were recorded during the period 0600 to 0700 hours. Afternoon observations were recorded during the period 1330 to 1530 hours. All males sampled were in reproductive condition. Observation periods for each group are listed in Table 5-2.

The isochrons of residence together with a histogram of the mean percentage of time allocated to the seven basic activities are plotted (Figs. 5-2 through 5-18) for each male studied.

Nursall (1977a) determined that a Redlip blenny spends 99% of its time within 50% of its territory, and about 80% of its time within 5% of its territory, without distinguishing its sex or reproductive condition. In addition, he found that the mean planar area of an individual's territory is about 0.50 m^2. Assuming that a nest cave represents less than 5% of the area of a territory, it was found that during the breeding period, males in reproductive condition spend a mean of $\overline{X} = 90.2 \pm 1.8\%$ of time within or next to the nest during the morning hours and spend $\overline{X} = 87.7 \pm 2.7\%$ of time within or next to the nest during the afternoon hours. The difference between these means is not significant (t-test, $P > .01$). The slight numerical difference between these means probably represents time spent foraging by the males during the afternoon hours. Nursall (personal communication, manuscript in preparation) in detailed analysis of a daily activity budget for *O. atlanticus* has demonstrated a significant increase in feeding activity in both sexes during the morning hours, reaching a more or less constant high level by noon, which is maintained throughout the afternoon. Feeding activity drops sharply during the hours

TABLE 5-2. Observation periods for eight males in reproductive condition (minutes).

Male	Breeding Period		Non-Breeding Period		Total
	Morning	Afternoon	Morning	Afternoon	
1	12	-	-	-	12
2	43	46	-	-	89
3	-	26	-	-	26
4	36	-	-	-	36
5	22	-	-	-	22
6	33	-	15	-	48
7	81	26	38	21	166
8	27	25	33	18	103
Total	254	123	86	39	502

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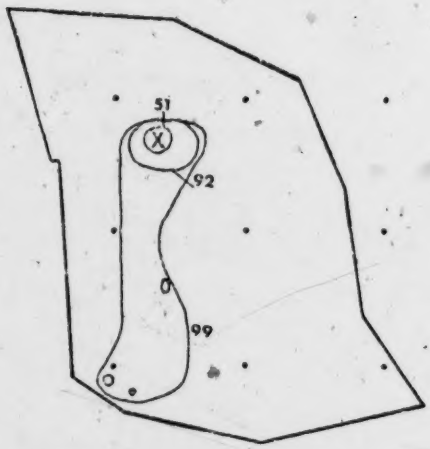
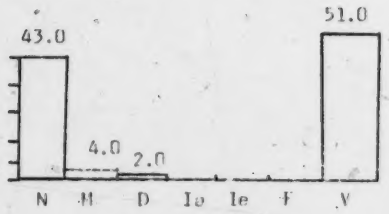
MALE 1 : am, BREEDING PERIOD

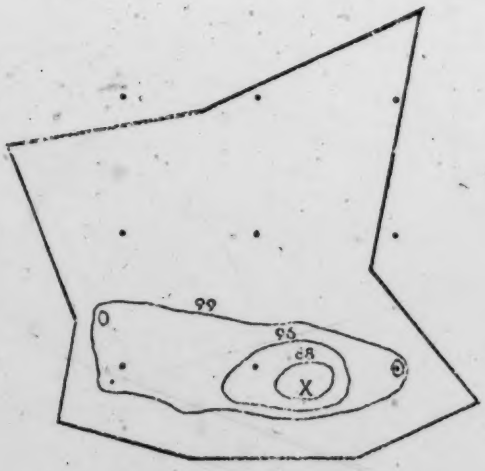
DATE : 6/10/76

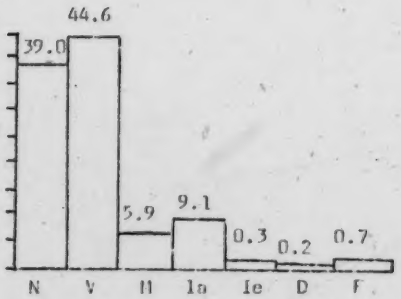




MALE 2 : am, BREEDING PERIOD

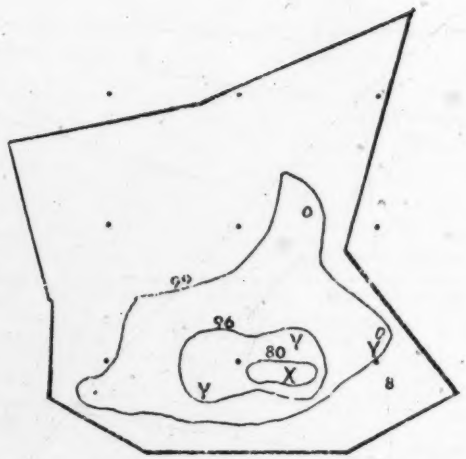
DATE : 6/30/76 - 7/6/76

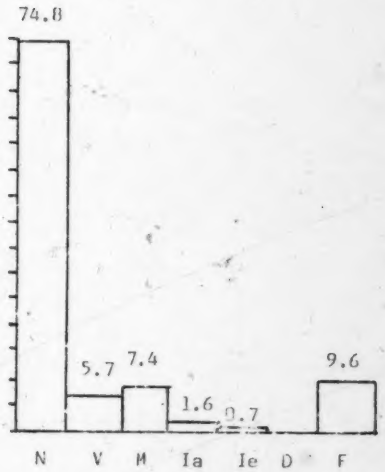




MALE 2 : pm, BREEDING PERIOD

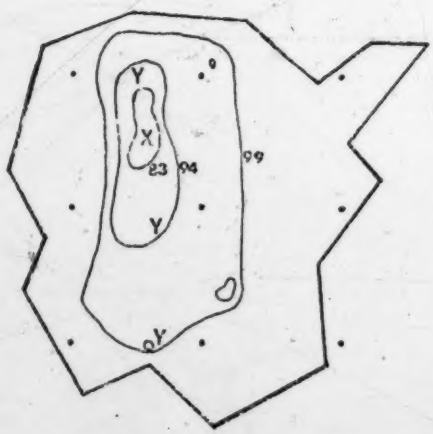
DATE : 6/29/76 - 7/1/76

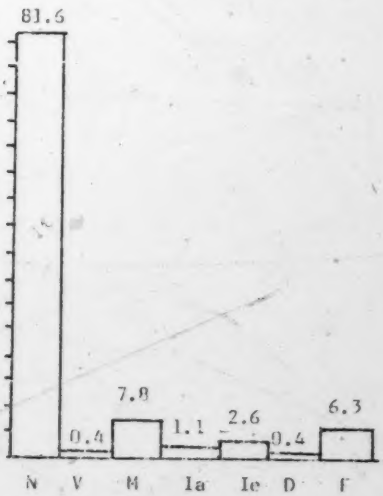




MALE 3 : pm, BREEDING PERIOD

DATE : 6/30/76 -, 7/1/76





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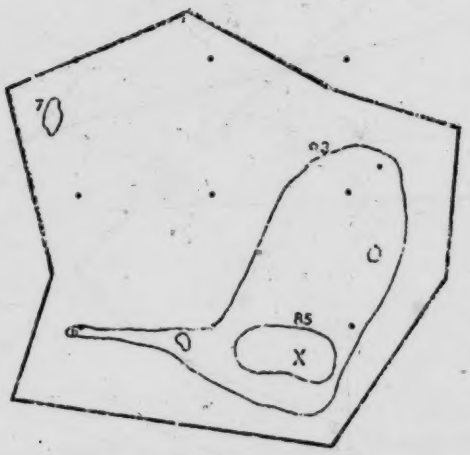

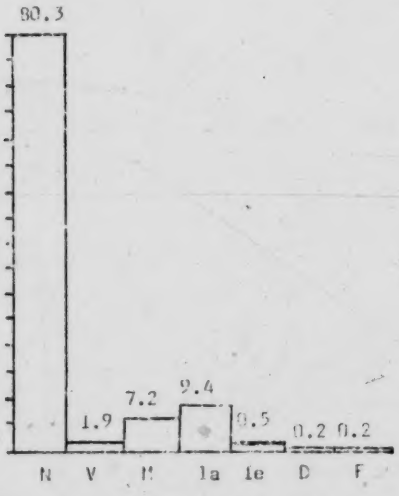

MALE 5 : ma, BREEDING PERIOD

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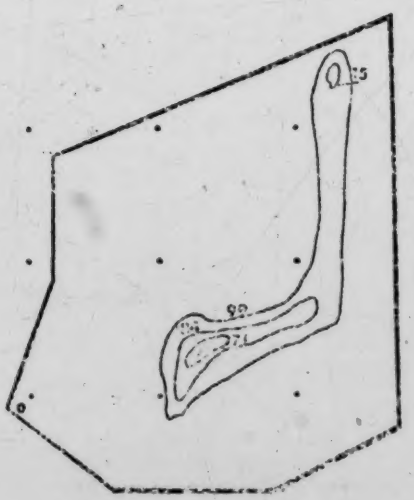
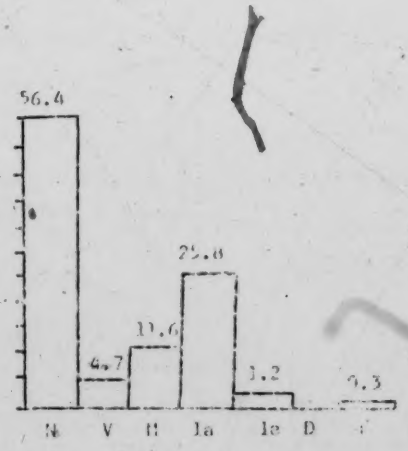
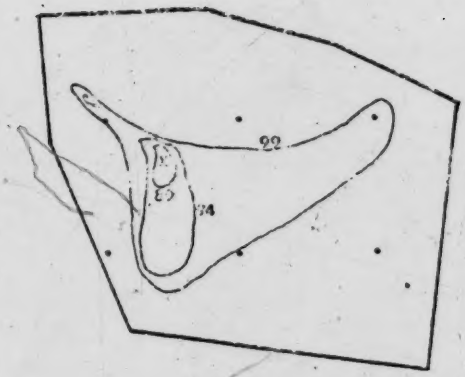
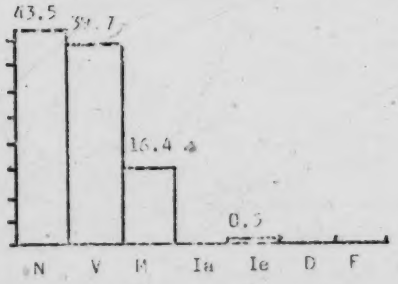




MALE 6 : am. BREEDING PERIOD

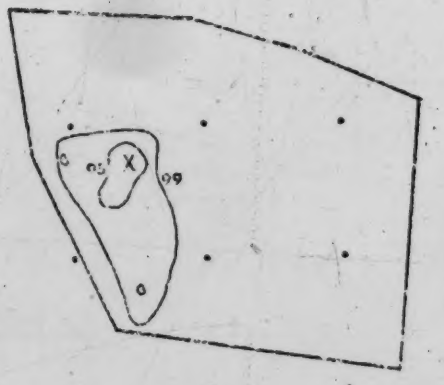
DATE : 8/14/76

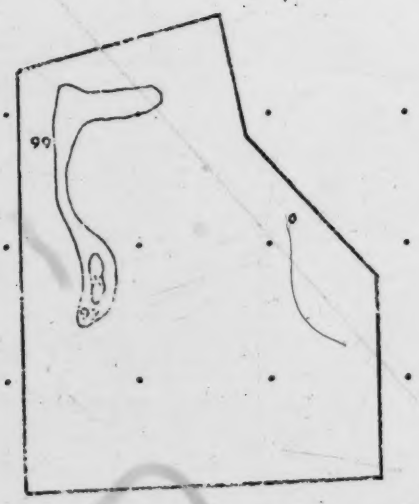




MALE 6 : am, NON-BREEDING PERIOD

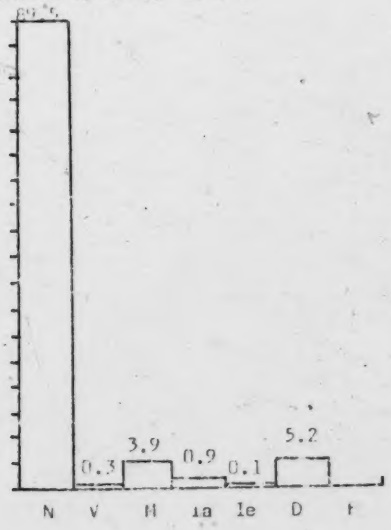
DATE : 8/17/76 - 8/19/76





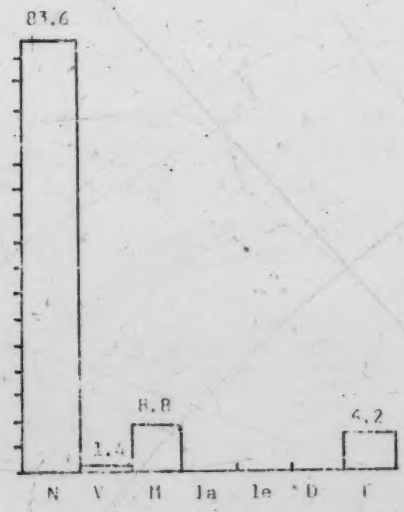
MALE 7 : ♂♂, BREEDING PERIOD

DATE : 1/31/77 - 2/7/77



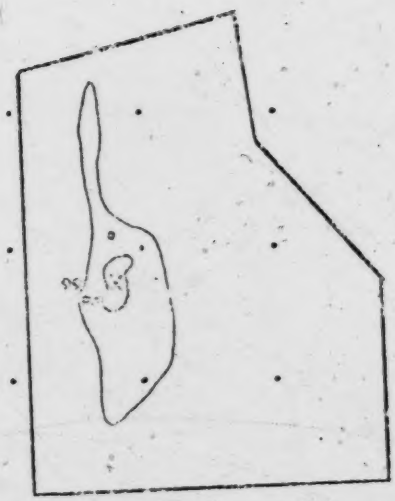
MALE 7 : ♂♂, BREEDING PERIOD

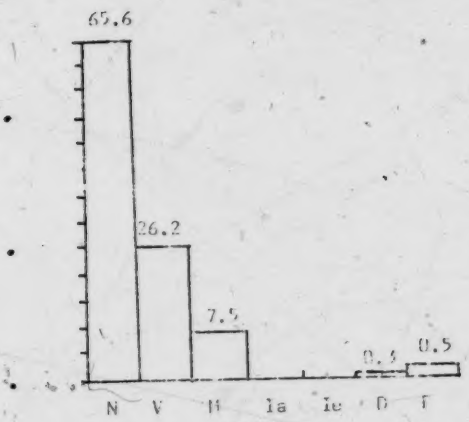
DATE : 1/31/77 - 2/7/77



HALL 7 : am, NON-BREEDING PERIOD

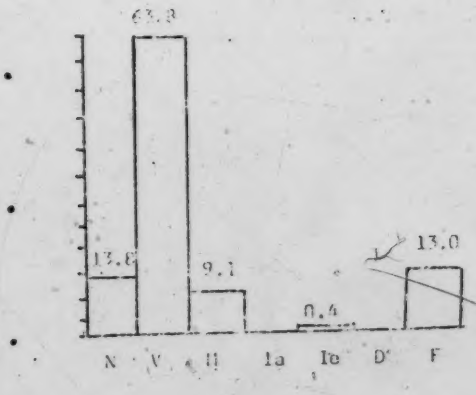
DATE : 2/14/77 - 2/18/77

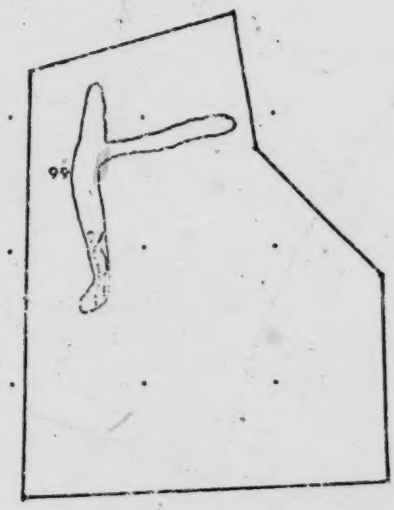




HALL 7 : pm, NON-BREEDING PERIOD

DATE : 2/16/77 - 2/18/77



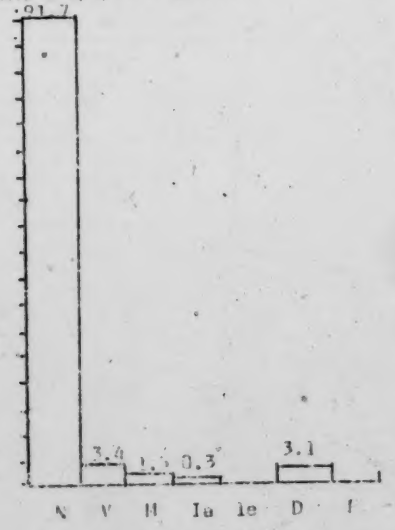


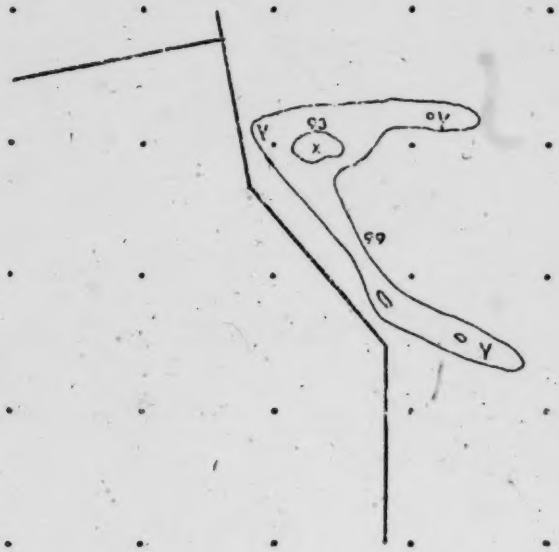
MALE 7 : am, BREEDING PERIOD

DATE : 2/26/77 - 3/2/77

MALE 8 : am, BREEDING PERIOD

DATE : 2/1/77 - 2/7/77





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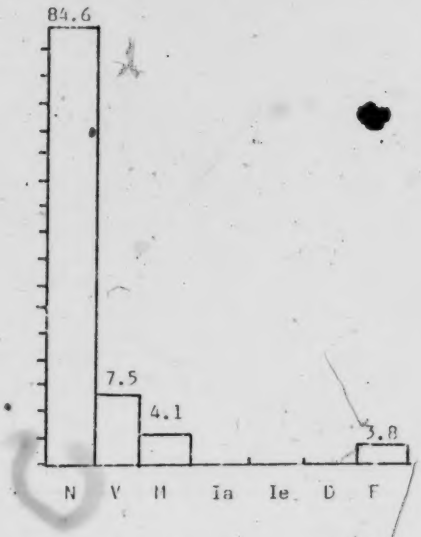
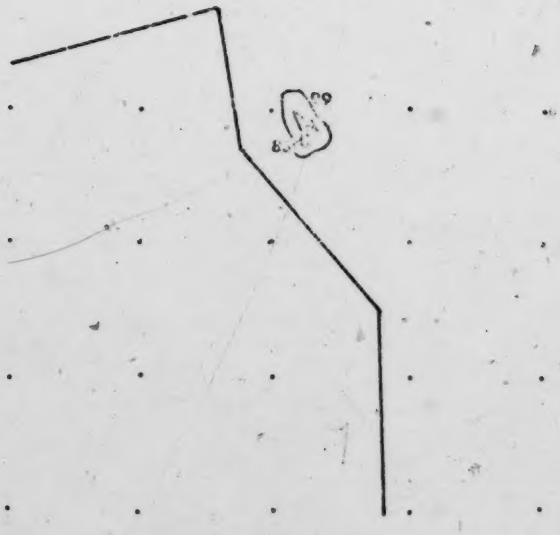
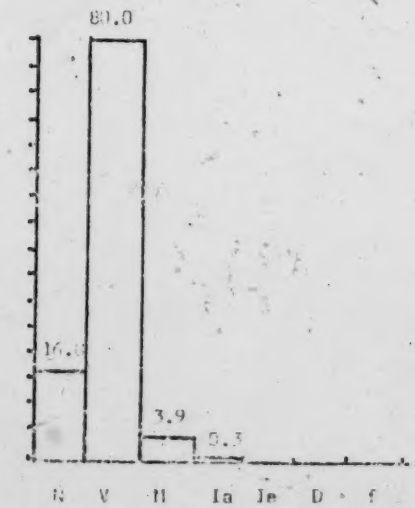
DATE : 2/1/77 - 2/7/77

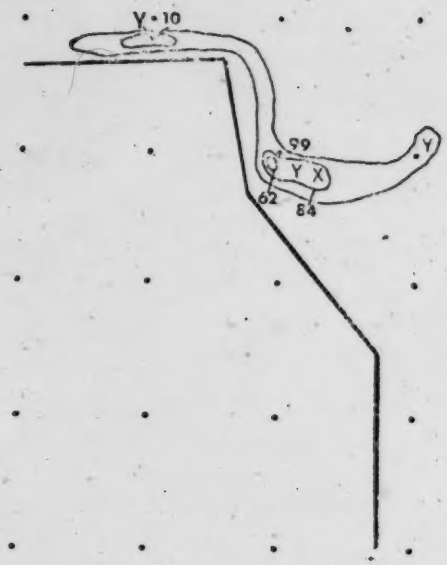




MALE 8 : am, NON-BREEDING PERIOD

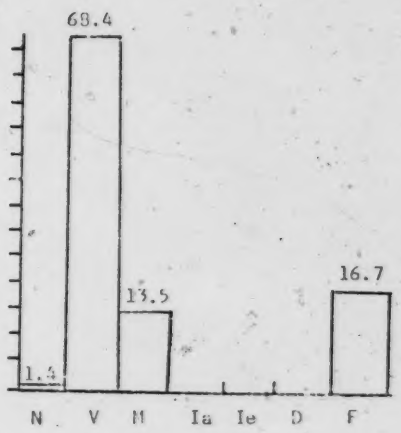
DATE : 2/14/77 - 2/18/77





MALE 8 : pm, NON-BREEDING PERIOD

DATE : 2/16/77 - 2/18/77



before sunset. These results came from an analysis of variance of arcsine $\sqrt{P}$ transformed data, followed by Duncan's test.

When they are not breeding, males in reproductive condition spend a mean of 93.4 ± 1.2% of time within or next to the nest during the morning hours. However, these males spend a significantly less amount of time (t-test, $P < .05$) within the nest or next to the nest ($X = 69.4\%$) during the afternoon of the non-breeding period. Analysis indicates that the percentage of time allocated to feeding in the afternoon during the non-breeding period by males in reproductive condition is significantly higher (t-test, $P < .05$) during any other of the remaining three groups.

An analysis using the Kruskal-Wallis test indicates that there is no significant difference ($P > .05$) within each of the four time periods (am, pm breeding period; am, pm non-breeding period) in the distribution of time allocated to the seven basic activities.

The percentage of time allocated to each of the seven basic activities between each of the four time periods was analyzed for significance using the Mann-Whitney analysis. Significant values were found ($P < .05$) for only two activities: feeding and moving.

Feeding activity was significantly higher during the afternoon for both the breeding period and the non-breeding period. Feeding activity during the morning hours is not common in males that are in reproductive condition. In addition, feeding activity was significantly higher ($P < .05$) for these males during the non-breeding period than during the breeding period. Males in reproductive condition appear to feed in specific locations within their

territories. These areas are marked for each male by the letter "Y" on the isochron maps. Feeding activity in breeding males is characterized by short (5-15 seconds) but frequent feeding trips to favored areas, followed by a direct return to the nest.

Males in reproductive condition appear to move about their territories most during the afternoon of the non-breeding period. Analysis indicates that movement is significantly greater ($P < .05$) during this period than during any of the other three periods examined.

Finally, evidence is presented to show that breeding activity is associated with the lunar cycle. Although males may exhibit physiological readiness (high GSI), they do not accept females into the nest until the first quarter/full moon phase of the lunar cycle. During the activity pattern study, spawning activity was monitored from January 31, 1977 through March 2, 1977 for two males in reproductive condition. The two males only accepted females into the nest from January 31 to February 7, and from February 26 to March 2. These periods coincided with the first quarter/full moon phase of the lunar cycle. Neither one of these males accepted females into the nest from February 13 through February 25. This period corresponded with the new moon phase. This evidence corroborates data collected during the spawning periodicity study (transect sampling, Chapter IV). The nest of one particular male along the transect was marked. Spawning activity at this site was monitored. The male was found to breed over three consecutive months (August, September, and October). However, females were only accepted during the full moon period of these

months. Although the males maintained the nest site, no females were seen spawning with the male during the new moon periods of these months.

CHAPTER VI

FECUNDITY ANALYSIS

Gibson (1969) described the general fecundity pattern among littoral fish species. He stated, "Fecundity varies with the species and with individual size, but generally it lies between a few hundred and several thousand eggs."

Ripe ovaries of four mature Redlip blennies (collected during June 1977 by Nursall) were dissected. An examination of these ovaries shows that asynchronous development is the rule.

In the ripe ovary, mature ova appear to be located on the ventral floor of the ovary, while ova at all stages of development occur randomly throughout the rest of the ovary.

The size distribution of ova obtained from a ripe ovary indicates that there was one group ready to be spawned ($\bar{X}$ = 0.68; $S\bar{x}$ = 0.01). These ripe ova were opaque, and all contained an oil globule. In addition, two other groups of ova ($\bar{X}$ = 0.36, $S\bar{x}$ = 0.009; $\bar{X}$ = 0.19, $S\bar{x}$ = 0.008) appeared to be undergoing vitellogenesis. This type of maturation of several groups of oocytes within an ovary is characteristic of fish species which exhibit iteroparity (Warner 1975) and it has been established (see Chapter V) that Redlip blennies spawn several times during a year.

Fecundity, which is defined as the total egg production/female (Simpson 1951), was determined by subsampling by weight the ovaries of 40 females. For each ovary, two subsamples of approximately 200 eggs

were weighed (dry weight). The dry weight of each ovary was recorded, and egg numbers were estimated by dividing the weight of the ovary by the unit mean weight of the subsamples.

Calculations of fecundity ranged from 1038 to 5900 eggs ($\bar{X}$ = 3073). Stephans *et al.* (1970) estimated the total egg production/female of *Hypsoblennius jenkinsi*, a California blenny, at 2900 eggs/female.

The estimates of fecundity for *O. atlantis* might be slightly exaggerated, since the relationship between these numbers and the number of eggs actually spawned depends on the survival rate of the oocytes to maturity. There may be some eggs left in the ovary of post-spawning females, which would degenerate (Warner 1974).

Egg production increases exponentially with length and can be expressed by the equation:

$$F = aL^b \text{ (Ricker 1975)}$$

where:

F = fecundity

L - total length

a,b = constants.

This relationship for *Ophioblennius atlanticus* is defined as:

$$F = 7.65 \times 10^{-4} L^{3.449} \quad \text{(Fig. 6-1).}$$

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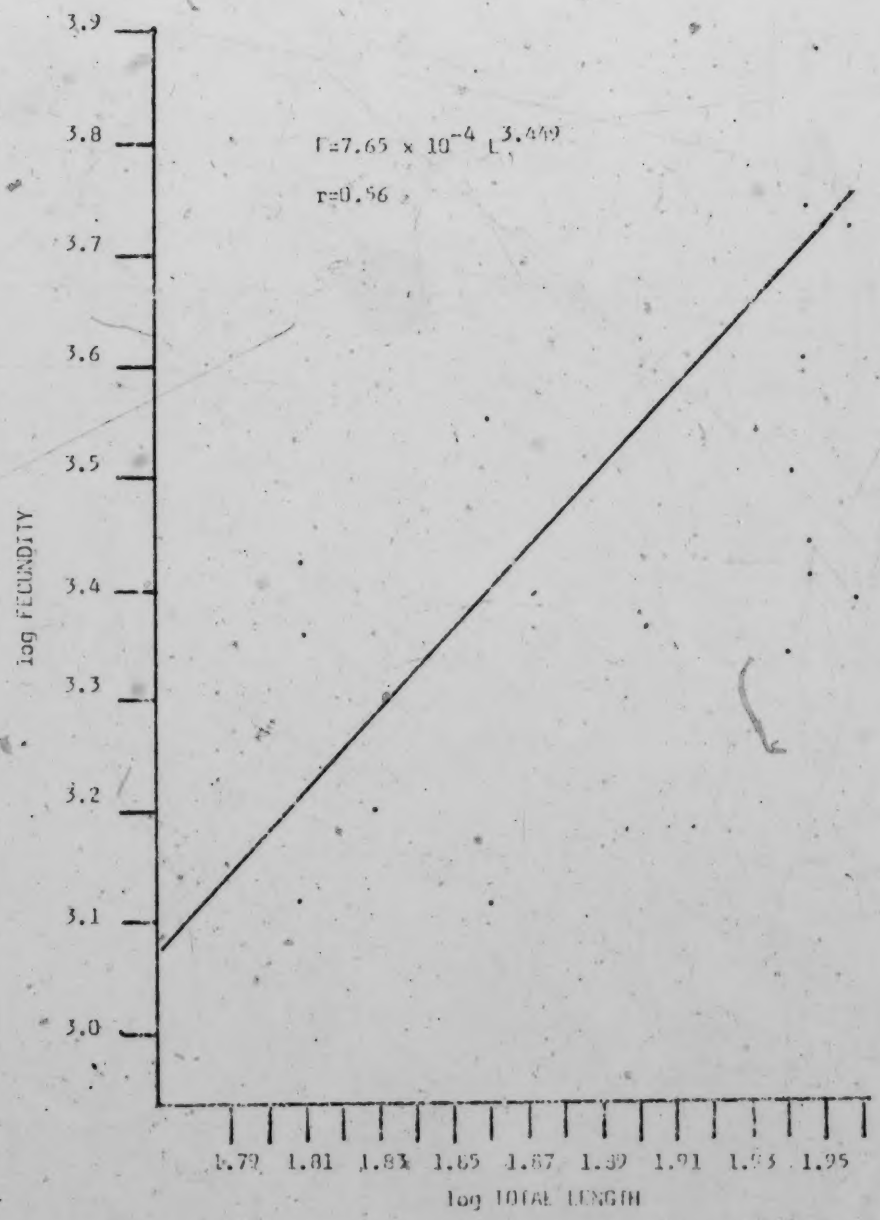
F=7.65 x 10^-4 L^3.449
r=0.96
3.9
3.8
3.7
3.6
3.5
3.4
3.3
3.2
3.1
3.0
log FECUNDITY
1.79
1.81
1.83
1.85
1.87
1.89
1.91
1.93
1.95
log TOTAL LENGTH

CHAPTER VII

ONTOGENETIC STUDIES

The early development of *Ophioblennius atlanticus* appears to be similar to that of other species of blennies. The eggs and early larval development have been described for several species of the Blenniidae. Breder and Rosen (1966) reviewed modes of reproduction in the blennies and give a general description of eggs from 15 species. Fishelson (1963) described larval development and metamorphosis in *Blennius pavo*. The eggs and larvae of *Hypsoblennius gilberti* are described by Losey (Dayneko 1975). Fishelson (1974, 1976) provided a detailed description of spawning and larval development of *Meiacanthus nigrolineatus*, a Red Sea blenny.

A general description of the ontogeny of *O. atlanticus* is reported. Results are based on field and laboratory observations.

Egg Development

Egg masses were collected from nests and were brought back to the laboratory for analysis. Hatching time was determined by observing egg development in the field. Spawning activity and development were monitored at six nest sites. New spawnings were recorded and the developing eggs were observed every 12 hours until hatching occurred. Egg color, gross embryonic features, and temperature of the water were recorded at each observation period. Water temperatures were taken by a hand-held thermometer, *in situ*.

The female deposits adhesive eggs along the walls and ceiling of the nest. The eggs are spherical, and adhere to the substrate by a disk which is composed of sticky filaments and appears to be an extension of the chorion. Newly spawned eggs measured about 0.68-0.75 mm in diameter. The perivitelline space measures approximately 0.06 mm around the yolk. The yolk, which occupies most of the egg, is yellow-brown. Fishelson (1976) reported that this sort of yolk coloration is characteristic of species which spawn in dark, sheltered nests and that the pigments may have a respiratory function.

The incubation period was determined to be 84-96 hours at 29°C. The exact hatching time was not determined because the eggs hatch during the evening hours when observations in the field were not possible. Newly hatched blenny larvae were found in surface tows as early as 1900 hrs., suggesting that hatching takes place soon after sunset. Thomson and Bennet (Gibson 1969) investigated reproductive activity in the oyster blenny, *Omobranchus anolius*. These authors reported that the majority of larvae of this species also hatch during the early evening hours.

General Development of the Embryo

12-24 hours

Egg color is yellow-brown. Embryo develops through blastula and gastrula. The head of the embryo becomes noticeable and light eye spots are visible.

24-48 hours

The eye spots are darkening. Twelve to sixteen melanophores have developed on the lateral side of the large yolk sac. A few (6-8) somites are now visible. The embryo is raised from the yolk sac and the caudal area is not attached to the yolk sac.

48-60 hours

The eyes are quite prominent. The cornea appears silvery. The yolk now occupies about one-half of the egg capsule. The auditory sac is visible and the primordial marginal fin is present. The number of somites appears to be increased (22 — based on one specimen). The mouth opening is also discernible at this stage.

60-84 hours

The melanophores have formed a "V" pattern on the ventral side of the embryo. The yolk material is further reduced (one-third of capsule). Pulsation of the heart is visible and movement of the embryo within the egg capsule is noticed.

The early larval period of the Redlip blenny has not been described. During this study, yolk-sac larvae were obtained by collecting egg masses in the field and then hatching them in the laboratory. Blenny larvae were also taken in surface plankton hauls. These larvae were identified by comparing them to known blenny larvae that had been hatched from eggs in the laboratory.

Attempts to culture the larvae either in the field or in the laboratory were not successful. Two types of system were employed to try to rear blenny larvae in the laboratory: a flow-through system

and a still-water system. The flow-through system (Fig. 7-1) consisted of a chamber and a gravel-sand filter. The chamber consisted of two elements. The first part was the container for the eggs. This apparatus was constructed from two pieces of PVC pipe (≃ 20 cm diameter). The diameters of these two pipes were slightly different from each other so that they could be secured to each other. One section of pipe functioned as a support stand for the apparatus. A piece of plankton netting (#6 mesh) was placed between the two sections of pipe and the eggs were then placed on top of the netting. The second part of the chamber was a 20-liter plastic bucket into which the container for the eggs was placed. The bucket had an overflow spout drilled into it so that the water level would not exceed the height of the egg container. This chamber was placed into the water table at the Bellairs Institute. The filter was a 20-liter plastic bucket, containing layers of beach sand and gravel (coralline rock). The filter was placed over the chamber. Sea water was continuously pumped into the filter, and the filtered sea water drained through an opening in the bottom of the filter, into the chamber. Egg masses which were near hatching (60-84 hrs.) were placed into the chamber. These egg masses were checked every 12 hours for two to four days. Although some hatching did occur, the larvae did not survive. This experiment was terminated after 11 unsuccessful attempts to rear the larvae after hatching.

The filter system was also used with a glass aquarium. Egg masses which were near hatching (60-84 hrs.) were placed in the aquarium. The aquarium was well oxygenated by an electric air pump,

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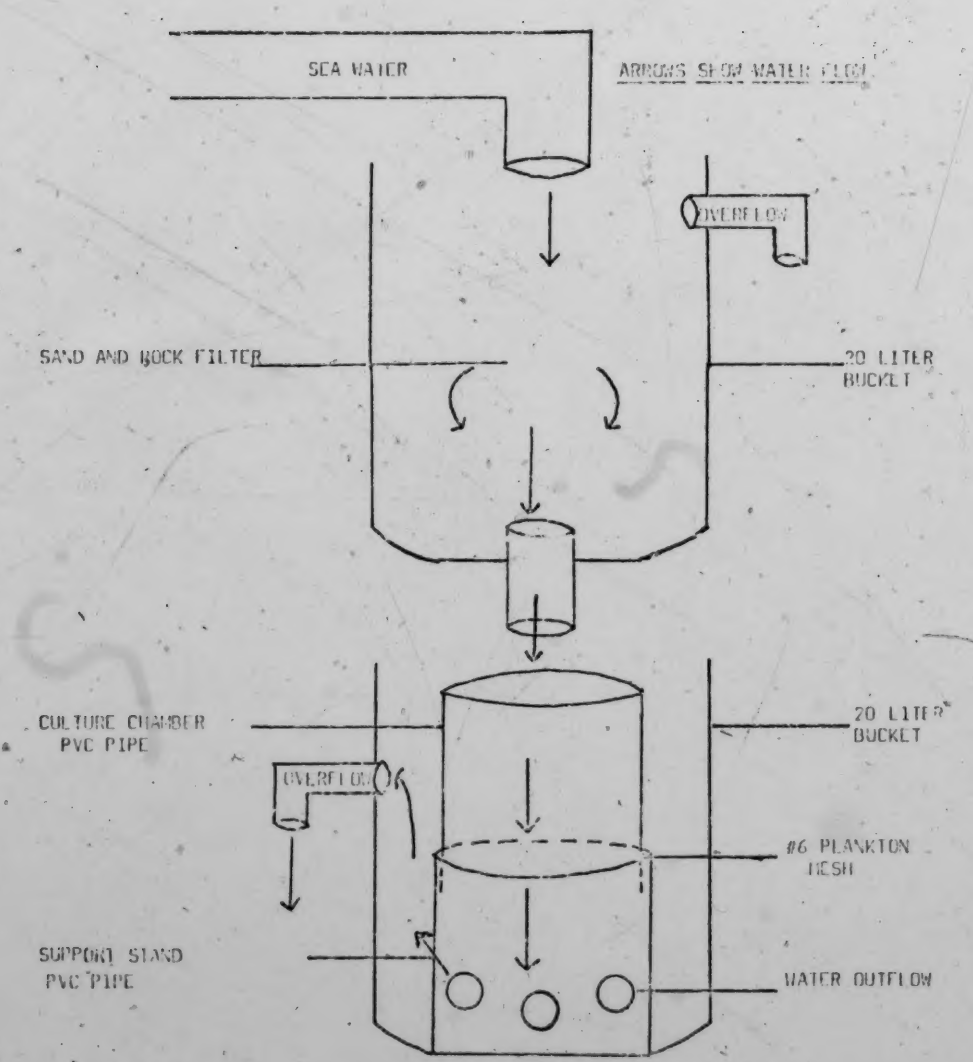
SEA WATER
ARROWS SHOW WATER FLOW
OVERFLOW
SAND AND ROCK FILTER
20 LITER BUCKET
CULTURE CHAMBER PVC PIPE
20 LITER BUCKET
OVERFLOW
#6 PLANKTON MESH
SUPPORT STAND PVC PIPE
WATER OUTFLOW

and the temperature was maintained at approximately 27°C. The aquarium was checked every 12 hours for two to four days for the presence of live blenny larvae. Although some hatching did occur, the larvae did not survive (4 trials).

A still-water system was constructed utilizing the Hinegardner (1969) culturing apparatus. Egg masses which were near hatching (60-84 hrs.) were placed into several culturing dishes. The sea water which was used to fill the culturing dishes of the Rinegardner apparatus had been passed twice through a millepore filter a week before using. Streptomycin, an antibiotic, was added to the sea water at the time of filtering. The sea water in the culturing dishes was changed daily. A 12-hour photoperiod was maintained, and the temperature in the culture dishes was kept at 29-31°C. Egg masses which were near hatching (60-84 hrs.) were placed into the culture dishes of the Hinegardner apparatus. Although most larvae did hatch, only one larva survived for more than 30 minutes. It remained alive for 26 hours.

An attempt was made to rear blenny larvae in the field. Three culturing apparatuses were constructed and were placed on the reef in shallow water (1-2 m). Each culture chamber consisted of a clear rectangular glass container (1' x 1' x 2') which was attached to a cinder block by several elastic bands. Egg masses which were near hatching (60-84 hrs.) were placed inside these culture chambers, and the chambers were covered with a plankton net (#6 mesh). The chambers (mesh-covered glass containers) were brought to the laboratory once a day for three days. The chambers were examined for the

presence of live blenny larvae which may have hatched from the egg masses. Dead blenny larvae were removed, and the chambers containing the egg masses were returned to the field. Four sets (12 trials) of experiments were conducted. No live blenny larvae were found in any of the culture chambers during these experiments, although many dead larvae were removed. This shows that blenny larvae did hatch within the chamber but that they did not survive long after hatching.

Two sets of experiments (6 trials) were conducted in which the male guard was placed inside the culture apparatus on the reef, with the egg masses. No other changes were made in the experiment. The presence of the male nest guard did not alter the results of these field experiments. No live larvae were observed, although many dead larvae were found in the culture chambers.

Hatchlings (Fig. 7-2) are well developed. They are transparent and are identified by a distinct melanophore pattern of the ventral side. The melanophores form a "≻" configuration which surrounds the gut. One or two melanophores are also present on the mediodorsal region of the larva. The primordial marginal fin is well developed. The yolk sac is quite large and the eyes are prominent. Hatchlings range from 1.5 to 1.7 mm. Swimming movements, which are weak, are enhanced by small pectoral fins.

The general features exhibited by the larva which had been cultured in the laboratory for 26 hours give some indication of the growth pattern of blenny larvae during the first day of development. Characteristics exhibited by the larva after 26 hours of development were:

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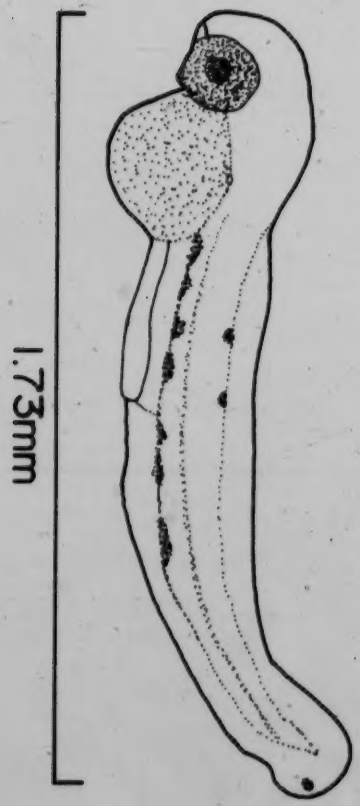
1.73mm

a). The larva measured 1.52 mm at hatching. After 26 hours the larva measured 1.80 mm.

b) Depletion of the yolk material. The yolk material represented less than 10% of the total yolk sac after 26 hours.

c) The pectoral fins were transparent and large. The fin rays were not yet distinguishable.

d) The melanophores on the ventral side had increased in diameter. Twenty-four melanophores were present on the ventral side.

e) An increase in proficiency of swimming ability is recognized. The larva tried to maintain itself near the surface. However, when movement ceased, the larva sank.

The larvae which were taken in the plankton tows (Fig. 7-3) appeared to be slightly more developed than the larva which had been cultured in the laboratory for 26 hours. Caudal dermal elements were conspicuous in planktonic larvae, which were probably not more than 48 hours old. Stephans *et al.* (1970) reported that the larvae of *Hypsoblennius jenkinsi* average 2.7 mm two days after hatching. Morphometric and meristic measurements of 40 Redlip blenny larvae which were taken in plankton tows are given in Table 7-1.

The larvae are most easily identified by the melanophore pattern. There is a unique pigment pattern on the ventral side of the larvae (Fig. 7-4). The melanophores form a " $>$ " configuration, the anterior arms of which surround the gut. Six or seven melanophores are present on each side of the gut and extend anteriorly to the pectoral region. Two to four melanophores are present on the ventral portion of the yolk sac. In addition, two to four melanophores are located on the dorsomedial region of the larvae (Fig. 7-5).

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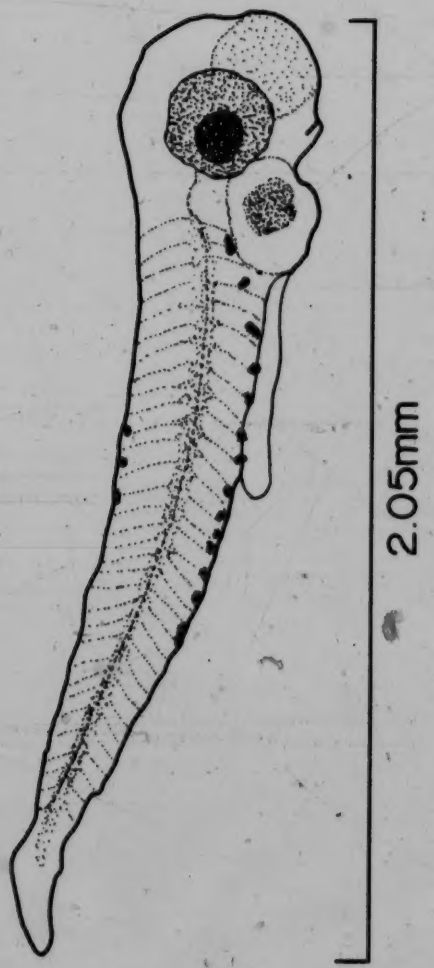
2.05mm

TABLE 7-1. Measurements of 40 Redlip blenny larvae taken in surface plankton hauls.

	Total Length	Snout to Vent Distance	Eye Diameter	Total Number of Myomeres	Myomeres	
					Pre-anal	Post-anal
$\bar{X}$	2.24	1.09	.25	33	20	13
Sx	0.03	0.02	.003	0.3	0.2	0.3
Range	1.85-2.5	.96-1.23	.22-.28	30-35	19-21	11-15

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CHAPTER VIII

RECRUITMENT

The salariine blennies, of which *O. atlanticus* is a member, have a characteristic larval stage that has its peak abundance offshore (Springer 1962, Stephans *et al.* 1970, Leis and Miller 1976). These pelagic larvae are so different from the adult form that they have been separately named in the past. Chapman (Strasburg 1953) uses the term *Ophioblennius* to denote the large larvae of *Cirrepectus*, another salariine genus. Reid (Strasburg 1953) proposed a new Hawaiian species, *Blenniella rhessodon*. The holotype of this proposed species was examined (Strasburg 1953), and found to be a large larva of *Istiblennius gibbifrons*. Springer (1962) describes such a pelagic stage for *Ophioblennius atlanticus*. Large blenniella larvae (30-38 mm TL) are pale torpedo-shaped fish which possess 10 large recurved canines. The dentition of these larvae is characterized by four procurved canines anteriorly in the upper jaw and recurved canines in the lower jaw. There is also a rearward curved canine on either side of the lower jaw which is separated from the anterior canines. Dr. Springer (personal communication) has collected these pelagic forms over deep water and in shallow water off the coasts of Dominica and the Virgin Islands.

As pointed out in the preceding section, only newly hatched blenny larvae or blenny larvae less than 2.5 mm TL were taken in plankton hauls. Redlip blennies are next encountered on the reefs as

juveniles. Clearly a considerable gap exists in our knowledge of the early life history and recruitment mechanisms of *O. atlanticus*. Therefore, an examination of recruitment mechanisms of blennies was instigated. Three life stages of Redlip blennies are recognized: larva (pre-metamorphosis), post-larva (undergoing metamorphosis), and juvenile (post-metamorphosis-immature).

It is hypothesized that there is an abundance of large blenny larvae in deep water off the coast of Barbados. These larvae eventually return back to shallow water, metamorphose, and are recruited into the adult population. Also, the occurrence of juvenile blennies on the reef throughout the study period, together with the fact that spawning is a year-round phenomenon, indicates that recruitment for blennies occurs throughout the year.

Repopulation Studies

Current opinion suggests that space for colonization may be the ultimate constraint placed on coral reef fish populations (Low 1971, Smith and Tyler 1972, Luckhurst 1972, Sale 1974). Therefore, the experimental control of space availability over time might be a useful method of examining recruitment and colonization in blennies.

Repopulation experiments, in which the availability of space was controlled, were carried out to determine both the length of the larval period and also the nature of colonization in Redlip blennies. Four small isolated coral heads (2 x 1 x 1 m) and also a 16 m^2 area on the main reef were chosen as the study sites. Two of the isolated coral heads (B1, B2) were adjacent to the main reef (< 1 m). It is

known that adult Redlip blennies may normally swim about a meter in order to transgress vacated territories. Therefore, colonization of coral heads B1, B2 by territorial expansion of adult blennies from the main reef is possible. The two remaining isolated coral heads (A1, A2) were located three or four meters from the main reef. Adult Redlip blennies do not normally transgress vacated territories which are three or four meters away. Therefore, it was expected that only larval recruits would colonize heads A1, A2.

The territories of all blennies on each study site were mapped. The procedure used to map the territorial boundaries of blennies is described by Nursall (1977a). Each blenny was subsequently speared and then placed into a separate plastic bag. The plastic bags were coded to ensure that each specimen could later be identified with a specific mapped territory. The study sites were treated with rotenone to ensure that all blennies were removed. Smith (1973) discussed rotenone treatment as a method of examining the resident fish populations from small patch reefs. Nursall (personal communication) noted that Redlip blennies are particularly susceptible to rotenone. Blennies were taken to the laboratory for examination of sex, weight, length, and gonad size. The sex ratio of the species was also estimated from the data obtained in this experiment. The results are listed in Table 8-1.

The sex ratio for the species appears to be 1:1. An analysis using the Mann-Whitney Statistic gives a non-significant value ($p > .01$) for the male and female populations.

TABLE 8-1. Repopulation Study: Analysis of sex ratio.

Study Site	Date Sampled	Description of Site	Depth (m)	Blennies Removed	Size Range (TL mm)	M:F
A1	10/06/76	isolated head	2	8	52-77	4:4
A2	10/18/76	isolated head	2	10	80-93	2:8
B1	10/13/76	isolated head	2	10	52-84	6:4
B2	10/26/76	isolated head	2	14	44-85	10:4
C	9/28/76]	16 m^2 area on main reef	3	27	39-89	12:15
Total						34:35

A post-larva (female-39.2 mm TL) was taken on September 28, 1976 (Fig. 8-1) from the 16 m^2 area (study site C). Although the anterior canines in both jaws of this female were present, the combteeth of this blenny were visible, indicating that this fish was undergoing metamorphosis (Springer 1962). The fish (Fig. 8-1) inhabited a crevice and was not visible on the study site. It was located by the application of rotenone to the study site subsequent to the spearing of all visible blennies on study site C.

Recruitment and colonization data were obtained by periodically visiting these study sites and recording the number and approximate size of any blennies which were inhabiting these sites. During these visits, rotenone was applied to the study sites to ensure that any cryptic larval or post-larval forms would also be collected. Study sites A2, B1, and B2 were examined 10 times over a period of six months (October-March). Study site A1 was sampled three times over the six-month period. In addition, study site A1 was again sampled on August 31, 1977 by Ruth Dubin. Therefore study site A1 was sampled over a period of 11 months. Since sufficient data were collected from study site C two weeks after clearing the site of all blennies, this site was only examined once during the experiment. The results are listed in Table 8-2.

Several hypotheses can be constructed from the data obtained during this repopulation study.

Although recruitment appears to be a year-round phenomenon, a seasonal peak is recognized. Study sites A1, A2, B1, and B2 were cleared during October 1976 of all resident fish, including 42 Redlip

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3
4

TABLE 8-2. Repopulation Study: Analysis of colonizers to Study Sites A1, A2, B1, B2, and C.

Study Site	Date First Sampled	Date Revisited	No. of Blennies on Study Site	Size Range	No. of Blennies Initially Removed
A1	10/06/76	11/06/76	0	-	8
A1	10/06/76	2/03/77	0	-	8
A1	10/06/76	3/24/77	0	-	8
A1	10/06/76	8/31/77	8	≈ 65	8
A2	10/18/76	11/13/76	0	-	10
A2	10/18/76	1/27/77	0	-	10
A2	10/18/76	3/25/77	0	-	10
B1	10/13/76	11/14/76	0	-	10
B1	10/13/76	1/27/77	0	-	10
B1	10/13/76	2/19/77	0	-	10
B1	10/13/76	3/26/77	0	-	10
B2	10/26/76	11/14/76	0	-	14
B2	10/26/76	1/27/77	1	52	14
B2	10/26/76	3/25/77	0	-	14
C	9/28/76	10/13/76	19	65-85	27

blennies. After six months of monitoring these study sites for the presence of colonizers, only a single blenny recruit (52 mm, site B1) appeared on any of these study areas. However, study site A1 was sampled again on August 31, 1977. Eight juvenile blennies, all members of the same size category (≈ 65 mm), were present. These facts suggest that these eight individuals were recruited to study site A1 during the same period. The facts also indicate that these fish were recruited as larvae, because study site A1 is located too far from the main reef to allow colonization through territorial expansion of adults from the main reef. In addition, the fact that eight blennies had been present on study site A1 on August 31 might be a significant issue since it was noted that eight blennies were removed from this coral head during October 1976. This fact suggests that eight might be considered the "equilibrium" number of blennies for study site A1, and therefore maximum recruitment to this area had taken place. The exact period that these blennies appeared on study site A1 is not known. Stephans *et al.* (1970) demonstrated that for *Hypsoblennius jenkinsi* there is a mass inshore larval settlement (36-40 mm) between August and October, and this period is approximately two or three months after breeding. Dayneko (1975) indicated that for *Hypsoblennius gilberti*, recruitment of small fish (39-46 mm) occurs in August, two months after the onset of spawning.

Assuming a larval period of two to three months for *O. atlanticus* and an initial growth rate of about 5 mm/month after metamorphosis (see Chapter IX), the eight blennies located on study site A1 would be five to seven months old. These fish would have hatched sometime

during February-April which is the peak spawning period. The period of maximum recruitment is assumed to be early to mid-summer.

In general, areas which are isolated or separated from the main reef are colonized only by larval forms. However, territories that have been vacated through predation or through artificial means are usually taken over by neighboring blennies (juveniles and adults) unless these vacated areas are isolated from the neighbors' territories.

A 16 m^2 area on the main reef (study site C) was cleared on September 29, 1976 of all resident fish species, including 27 Redlip blennies. Two weeks later the area was visited. Nineteen Redlip blennies were recorded within the 16 m^2 area. These 19 blennies ranged in size from ≈ 65 to ≈ 85 mm. No larval or post-larval forms were visible on study site C. Nursall (1977a) provided experimental evidence that territories which have been vacated are subsequently invaded by mature Redlip blennies. He did not see larval forms taking over vacated territories. The data obtained from study site C show mature neighboring blennies rather than larval forms encroaching upon and finally establishing themselves within the vacated area.

It must not be inferred, however, that larval forms only colonize isolated areas and do not colonize areas which are inhabited by the adults. Nursall (1977a) demonstrated that small, immature forms take up "interstitial" territories between the adults and proposed that these "interstitial" territories are expanded as the blenny grows. This author postulated "that the occupation of an interstitial territory is probably the result of a post-larval individual finding a

refuge which is a hole or crevice within which it spends most of its time." A small metamorphosing post-larva was found within a crevice at study site C. This individual occupied an area which was surrounded by adult territories. This fact, together with the observation that very small juveniles (40-50 mm) that occupy interstitial territories have a tendency to stay in or near a specific crevice, suggests both that larval forms are the agents of dispersal and also that these larval forms eventually take up residence within interstitial territories between areas occupied by adults.

The data from study sites A1, A2, B1, and B2 show that only larval forms were successful in colonizing isolated areas. The eight blennies that colonized study site A1 were all juveniles. It is improbable that these eight individuals could have immigrated to site A1 from the main reef because site A1 was located too far from the main reef to permit normal transgression of vacated space. Therefore these blennies had to be recruited as larval forms.

A single blenny (female, 52 mm) colonized site B2. This fish was first noticed on January 27, 1977, which was three months after the site had been cleared of all blennies. This female had a tendency to remain in or very close to a specific crevice. The blenny was never seen more than 15 to 30 cm from the crevice. The behavior of the fish indicated that it was young. The female occupied a small interstitial type territory on the side of the coral head opposite the main reef. Although study site B2 was quite close to the main reef, these facts suggest that the female was recruited as a larval form.

It is known that adult Redlip blennies normally transgress and take over vacated neighboring territories (Nursall 1977a). Transgressors may travel a meter in order to take over vacated space. However, over a six-month period, no adults from the main reef had colonized study sites A1, A2 which were located less than one meter from the main reef. It is hypothesized that transgression by adults from the main reef to study sites A1, A2 did not occur because of the discontiguity of the areas and the discontinuity of the reef structure. Both study sites were separated from the main reef by a sand barrier and open water. Predation pressure is strong in coral reef fish communities (Hobson 1972). Redlip blennies are bottom-dwelling fish which exhibit abnormal swimming behavior in open water. Also, they appear conspicuous when viewed on light backgrounds such as sand. Therefore adult blennies which attempt to cross open water or a sand barrier are out of their normal environment and are exposed to predation. It is possible that adult Redlip blennies from the main reef did attempt to transgress the vacated territories on sites A1, A2, but were unsuccessful because of high predation pressure.

Substrate Sampling

Leis and Miller (1976) indicated that the fish larvae of many Hawaiian reef fish with demersal eggs undergo direct development and settle out of the plankton at a relatively small size (< 10 mm). Although it has been shown that the larvae of *O. atlanticus* do not undergo direct development (Springer 1962), it has not been determined when the larvae settle out of the plankton. The fact that a

metamorphosing post-larva was found living within the substrate does not establish when that larva settled. In order to ascertain if the larvae of *O. atlanticus* settle out of the plankton at an early age and undergo development within the crevices of the reef structure, substrate samples were collected and examined for the presence of newly hatched blenny larvae.

Seventeen substrate samples consisting of live coral and coralline rock were collected. These samples ranged from 1/3 to 1/2 m in diameter and were about 30 cm in height. Seven samples were collected in September and 10 samples were collected in October. It was expected that if blenny larvae settle very early and undergo development within the substrate they would be found in the substrate samples, since breeding was seen to occur during September and October and recruits would be present. The samples were collected by placing heavy plastic bags over areas of substrate, tying off the plastic bags, and severing the samples from the reef with a hammer. These samples were taken to the laboratory for analysis. They were washed with both water and 10% formalin. The washings were filtered through a #6 plankton mesh and were examined under a dissecting microscope. No blenny larvae were found in any of the substrate samples.

As stated earlier in this section, the salariine blennies as a group have a pelagic larval stage that has its peak abundance offshore. Because no small blenny larvae were found within the substrate samples, and because large pelagic larvae have been collected by Springer, it is hypothesized that Redlip blennies are recruited as large unmetamorphosed larvae (35-40 mm) and do not settle early in their development.

It is also hypothesized that transformation and metamorphosis of the pelagic forms is induced by substrate contact and occurs within a crevice of the reef structure. This is evidenced by the presence of the large metamorphosing female that was found living within a crevice of the reef.

Discussion

Mature Redlip blennies hold permanent territories and are not the normal agents of species dispersal. Recruitment appears to be the result of settlement by large unmetamorphosed pelagic larvae which are two or three months old.

Although there are prevailing westerly ocean currents off the coast of Barbados, Powles (1975) has determined that recruitment of reef fish to Barbados inshore areas is a result of production from these inshore populations rather than from populations of reef fish in other areas of the western Atlantic or eastern Caribbean. Emery (Powles 1975) hypothesized that a von Karmen vortex system does exist in the wake of Barbados. Powles (1975) suggested that these neritic and oceanic current eddies act as a retention system and as a return mechanism for reef fish larvae from Barbados.

Assuming that these larval retention mechanisms do exist around Barbados, then the lengthening of the planktonic larval period and the postponement of metamorphosis is a clear advantage since suitable substrate for settlement would not be encountered by blenny larvae until they arrived back in shallow water. Larval fishes of the Caribbean families Serranidae (Smith 1961) and Pomacentridae (Emery

cited by Powles 1975) have been shown to postpone metamorphosis and settlement under conditions where suitable stimuli for settlement were absent.

It is hypothesized that there is an abundance of unmetamorphosed blenny larvae in deep water off the coast of Barbados. Sale (Leis and Miller 1976) hypothesized that oceanic current eddies are a return mechanism for Hawaiian reef fish larvae. Leis and Miller (1976) determined that the Hawaiian salariine blennies have a modified pelagic stage which has its peak abundance 10-12 km offshore.

It is also hypothesized that although recruitment appears to be a year-round phenomenon, a seasonal recruitment peak (early to mid-summer) is recognized. The exact time of this peak is not determined. Several authors have discussed seasonal recruitment peaks for Caribbean reef fish families. Luckhurst and Luckhurst (1977) investigated recruitment patterns of 16 species of coral reef fishes from Curaçao. They recognized two seasonal peaks (March-May, September-November) in abundance of recruits for species examined. Powles (1975) described seasonality in larval abundance of inshore reef fish families from Barbados. He concluded that there are two seasonal peaks in abundance of inshore reef fish families: March-May and August-October. In addition, Watson and Leis (1974) examined larval catch rates for Hawaiian reef fish. They found a fall and a spring peak for most inshore reef fish families. However, they examined larval abundance rates of four species of blennies and reported that each of the four species has only one seasonal recruitment peak although breeding in these species is a year-round phenomenon.

CHAPTER IX

AGE AND GROWTH

Age was estimated by plotting the frequency of the ratio of weight:length for 274 Redlip blennies. Beyond metamorphosis, growth is isometric for both sexes with respect to length-weight. Data for males (103) and for females (171) were recorded separately. The fish were collected from June 7, 1976 through March 26, 1977.

The otoliths of nine mature specimens were examined for the presence of seasonal rings. This method of age determination was unsuccessful because the hyaline bands and opaque bands of the sagitta could not be recognized. Pannella (1975) examined otolith growth patterns of several species of tropical fishes from Puerto Rico. He concluded that growth rings of most small tropical species were impossible to detect. In addition, he determined that the hyaline and opaque bands of tropical fishes may represent daily, fortnightly, or monthly patterns and therefore, without a check, the use of hyaline and opaque bands in tropical fish otoliths as indicators of annual periodicity can be misleading.

The weight:length frequency histograms are plotted for males (Fig. 9-1) and for females (Fig. 9-2). Small sample sizes require both that the data be grouped in two-month intervals and by percentage-frequency distribution. No data are available for December 1976 and January 1977. The raw data which were used to estimate the weight:length ratios are presented in Appendix I. The mean weight:length ratio of the modal peaks of the two-month intervals

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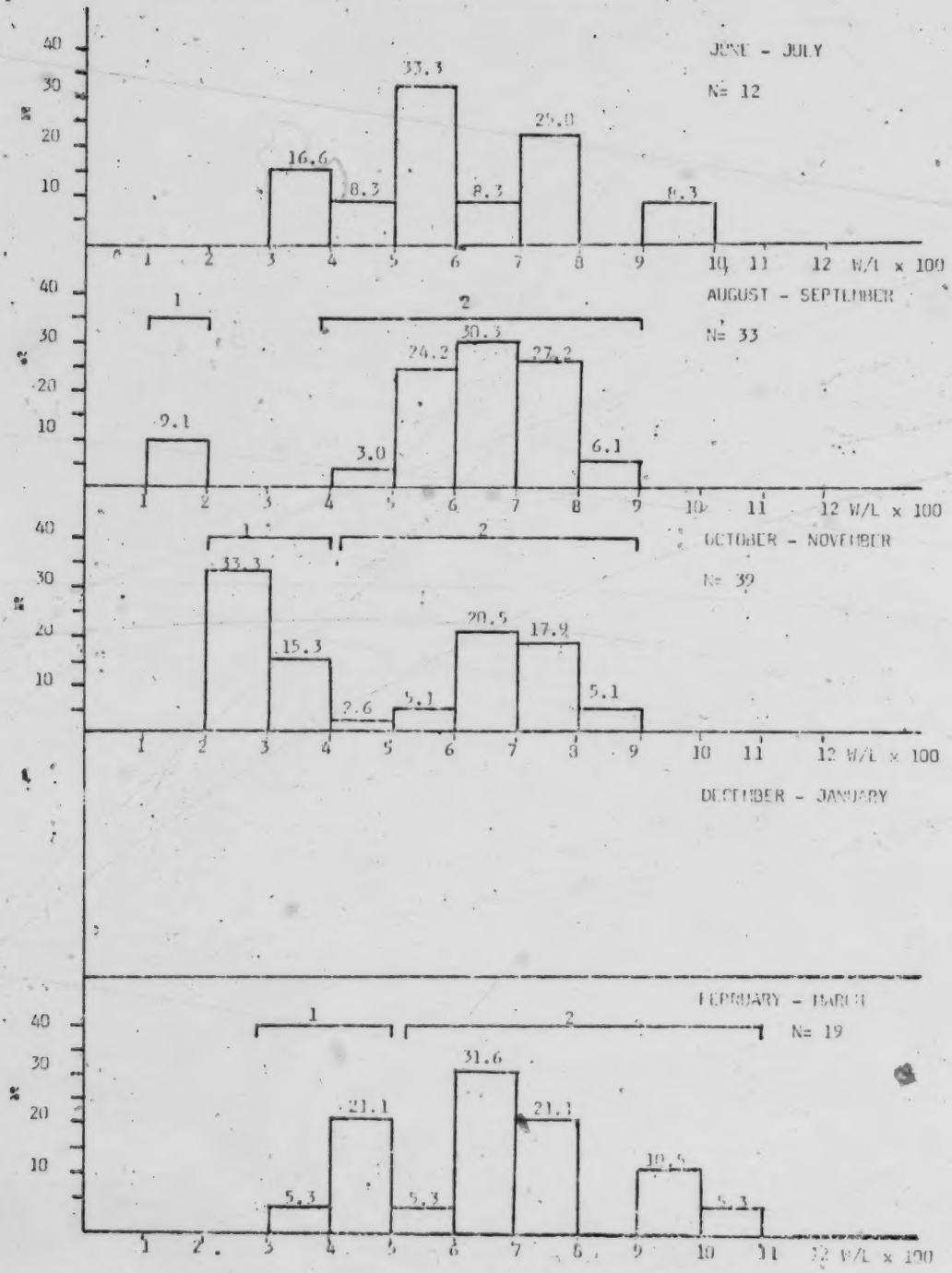
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16.6
8.3
33.3
8.3
25.0
8.3
AUGUST - SEPTEMBER
N= 33
9.1
3.0
24.2
30.3
27.2
6.1
OCTOBER - NOVEMBER
N= 39
33.3
15.3
2.6
5.1
20.5
17.9
5.1
DECEMBER - JANUARY
FEBRUARY - MARCH
N= 19
5.3
21.1
5.3
31.6
21.1
10.5
5.3
W/L x 100

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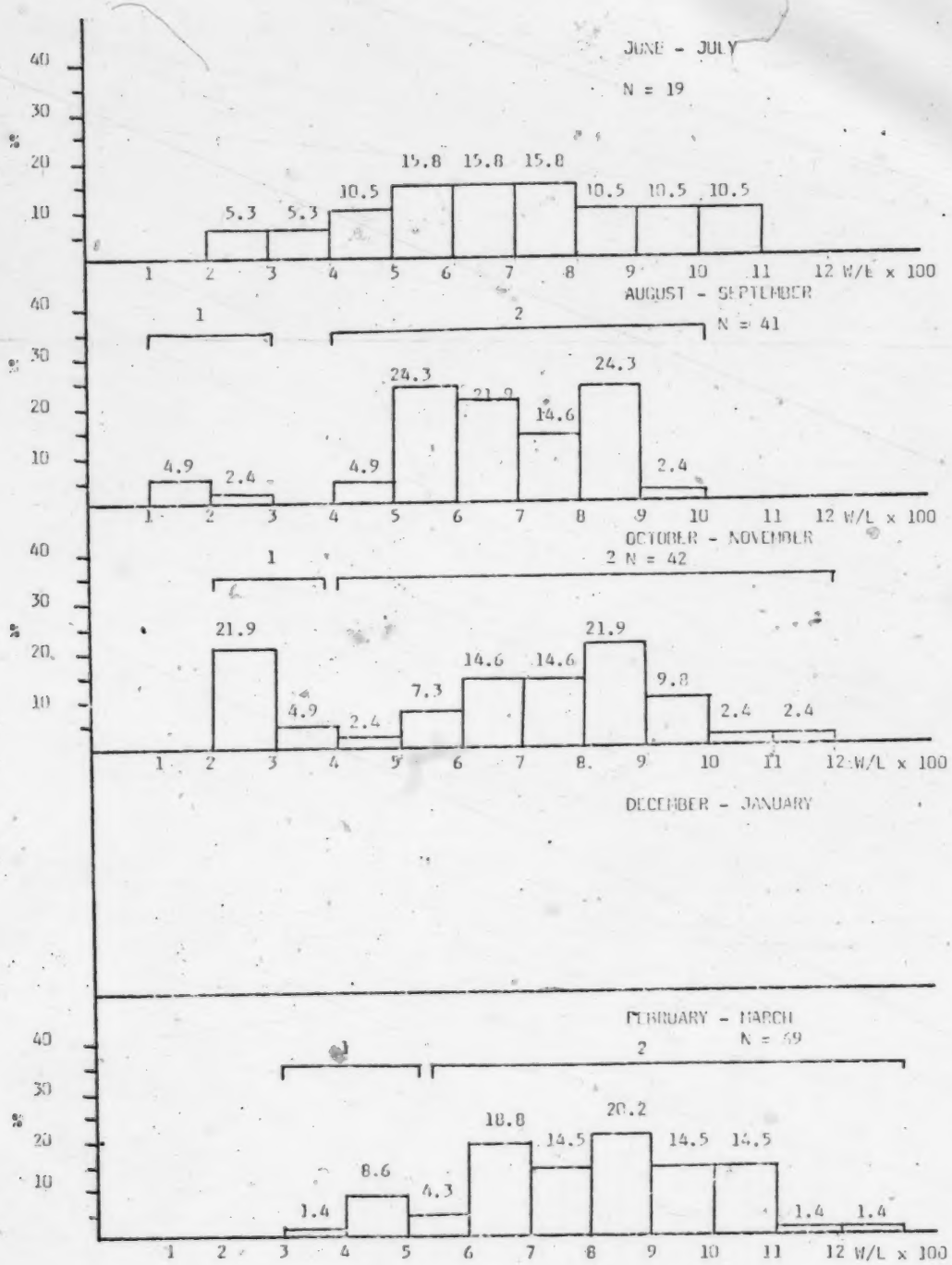
JUNE - JULY
N = 19
5.3 5.3 10.5 15.8 15.8 15.8 10.5 10.5 10.5
1 2 3 4 5 6 7 8 9 10 11 12 W/L x 100
AUGUST - SEPTEMBER
N = 41
4.9 2.4 4.9 24.3 21.9 14.6 24.3 2.4
OCTOBER - NOVEMBER
N = 42
21.9 4.9 2.4 7.3 14.6 14.6 21.9 9.8 2.4 2.4
DECEMBER - JANUARY
FEBRUARY - MARCH
N = 69
1.4 8.6 4.3 18.8 14.5 20.2 14.5 14.5 1.4 1.4
%

for males and for females are similar: a *t*-test between the male and female weight:length ratios shows no significant difference ($P > .05$). Therefore, the male-female data were combined and the weight:length ratio histogram for the combined data is plotted in Figure 9-3.

Two modal peaks are hypothesized from the weight:length frequency histograms. Age is inferred by assuming that the two modal peaks from the histograms represent a 2-year life span for blennies. Small samples taken within a limited time span necessitate that this conclusion be stated in the form of an hypothesis. More data, as well as an objective method of age determination (growth rings) are required before any firm conclusions can be reached.

The length-frequency data for males and the length-frequency data for females were fitted to the von Bertalanffy (Ricker 1975) theoretical growth equation. The length-frequency data were obtained from the weight:length data. The theoretical growth curve for males is plotted in Figure 9-4, and the theoretical growth curve for females is plotted in Figure 9-5. The numbers along the ordinate represent time in months.

The mean lengths at various ages for males and for females are similar: a *t*-test between male and female lengths shows no significant difference ($P > .01$). Therefore the growth data for males and for females were combined. The combined data were fitted to the von Bertalanffy (Ricker 1975) theoretical growth equation:

$$L_t = L\ (1-3^{-k\ (t-t_0)})$$

where: L_t = Total length at time
L = Theoretical maximum length
t = Time in years
k, t_0 = Constants .

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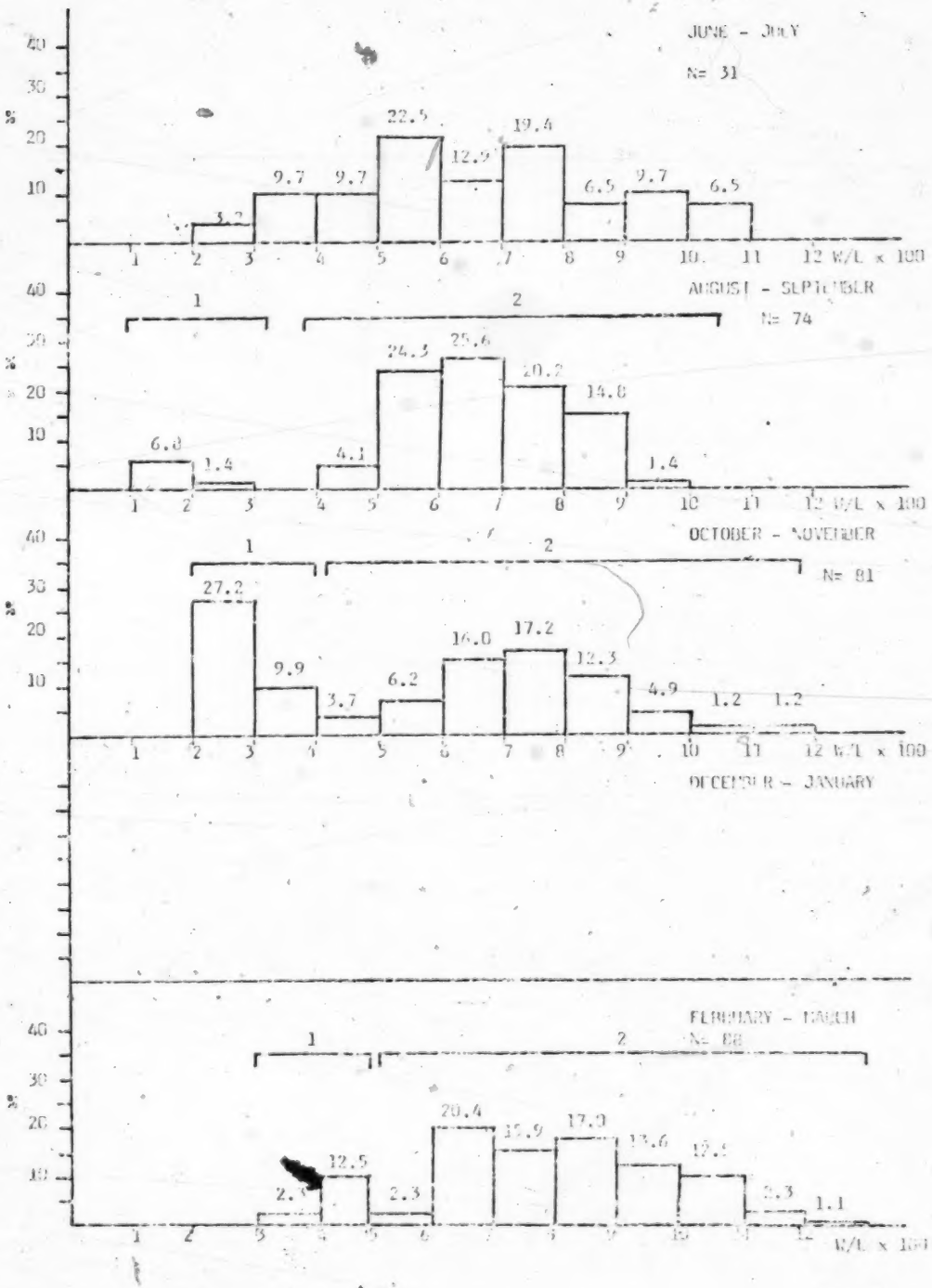
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22.5
19.4
12.9
9.7
9.7
6.5
9.7
6.5
3.2
W/L x 100
AUGUST - SEPTEMBER
N= 74
24.3
25.6
20.2
14.8
6.8
4.1
1.4
1.4
OCTOBER - NOVEMBER
N= 81
27.2
9.9
3.7
6.2
16.0
17.2
12.3
4.9
1.2
1.2
DECEMBER - JANUARY
FEBRUARY - MARCH
N= 88
20.4
17.0
13.6
12.5
2.3
2.3
1.1
%

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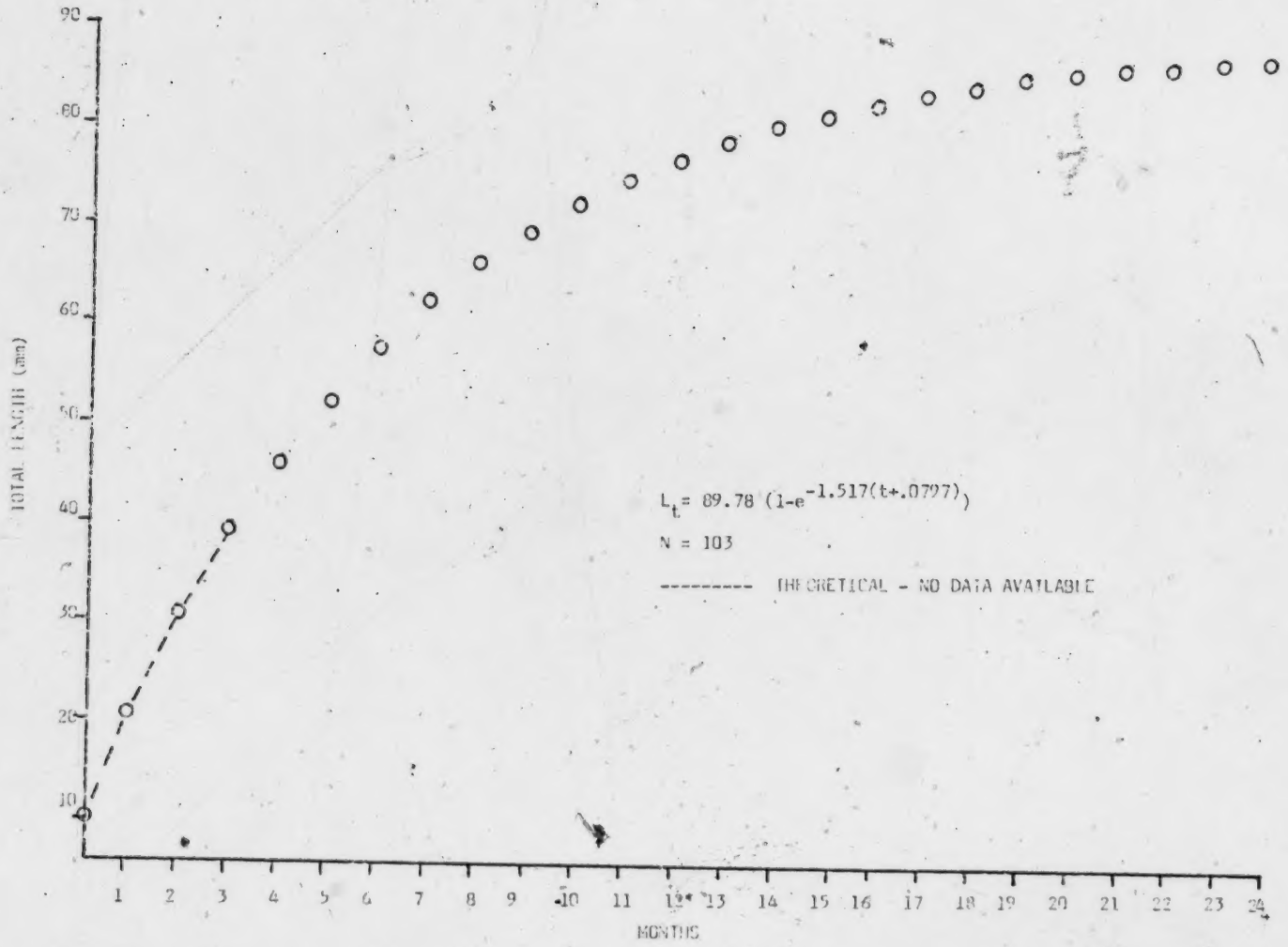
90
80
70
60
50
40
30
20
10
TOTAL LENGTH (mm)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
MONTHS
$L_t = 89.78\ (1-e^{-1.517(t+.0797)})$
N = 103
--------- THEORETICAL - NO DATA AVAILABLE

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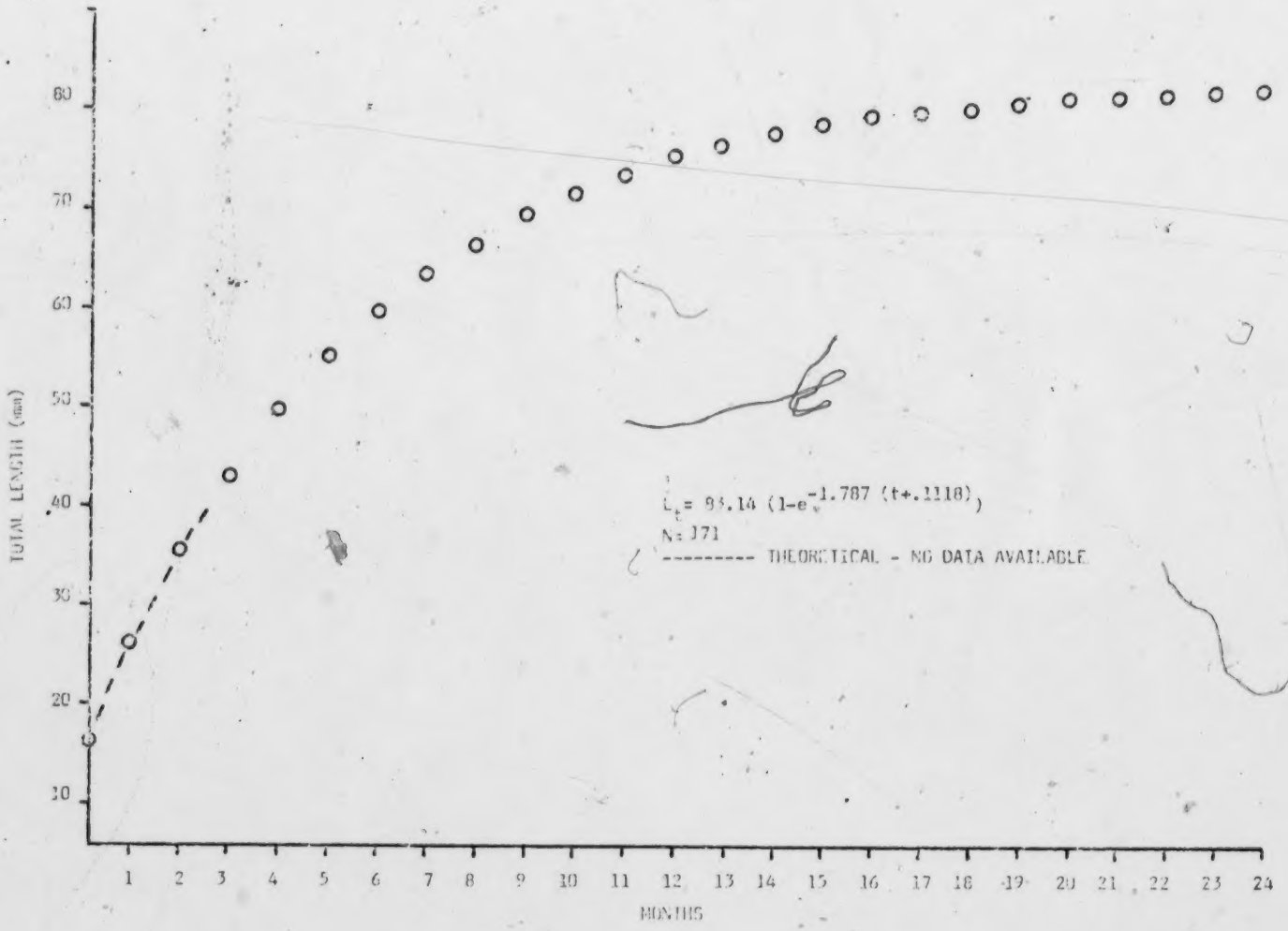
TOTAL LENGTH (mm)
10
20
30
40
50
60
70
80
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
MONTHS
$L_t = 93.14\ (1-e^{-1.787\ (t+.1118)})$
N: 171
--------- THEORETICAL - NO DATA AVAILABLE

These parameters were determined by the Abramson (1971) method. The combined data fit the growth equation as follows:

$$L_t = 84.81\ (1\text{-}e^{-1.8293\ (t+.0201)})\ \text{(Fig. 9-6)}.$$

The growth rate appears to be quite high (5-6 mm/month) during the first year and then is drastically reduced (< 1 mm/month) for the remainder of the individual's life span.

This high growth rate for young individuals appears to be consistent with the results of tagging experiments carried out during October and November 1976. Twenty small Redlip blennies (42-68 mm) were tagged and measured in the field. Only one specimen was re-examined for an increase in length. This individual was a male (48 mm) and exhibited a growth rate of 5.8 mm over a six-week period.

High growth rates have been determined for several species of Caribbean reef fish. Randall (1962) examined growth rates for tagged individuals of the families: Acanthuridae, Serranidae, Chaetodontidae, and Scaridae. He reported high growth rates for young individuals: Acanthuridae, 6.38 mm/month; Chaetodontidae, 6.47 mm/month; Scaridae, 12.0 mm/month. The growth rates for large (adult) individuals rapidly decline (< 1 mm/month) in all of these families. Allen (1975) reported growth rates in juveniles of several pomacentrid species of up to 13 mm/month. In addition, Strasburg (1953) tagged juveniles of a Hawaiian blenny, *Istiblennius zebra*. This author listed a mean growth rate of 5.3 mm/month over a size range of 24-96 mm. The growth range from 24-96 mm represented 13 months of growth.

Tropical fish species, in general, exhibit much higher growth rates during the early stages of development than do temperate species.

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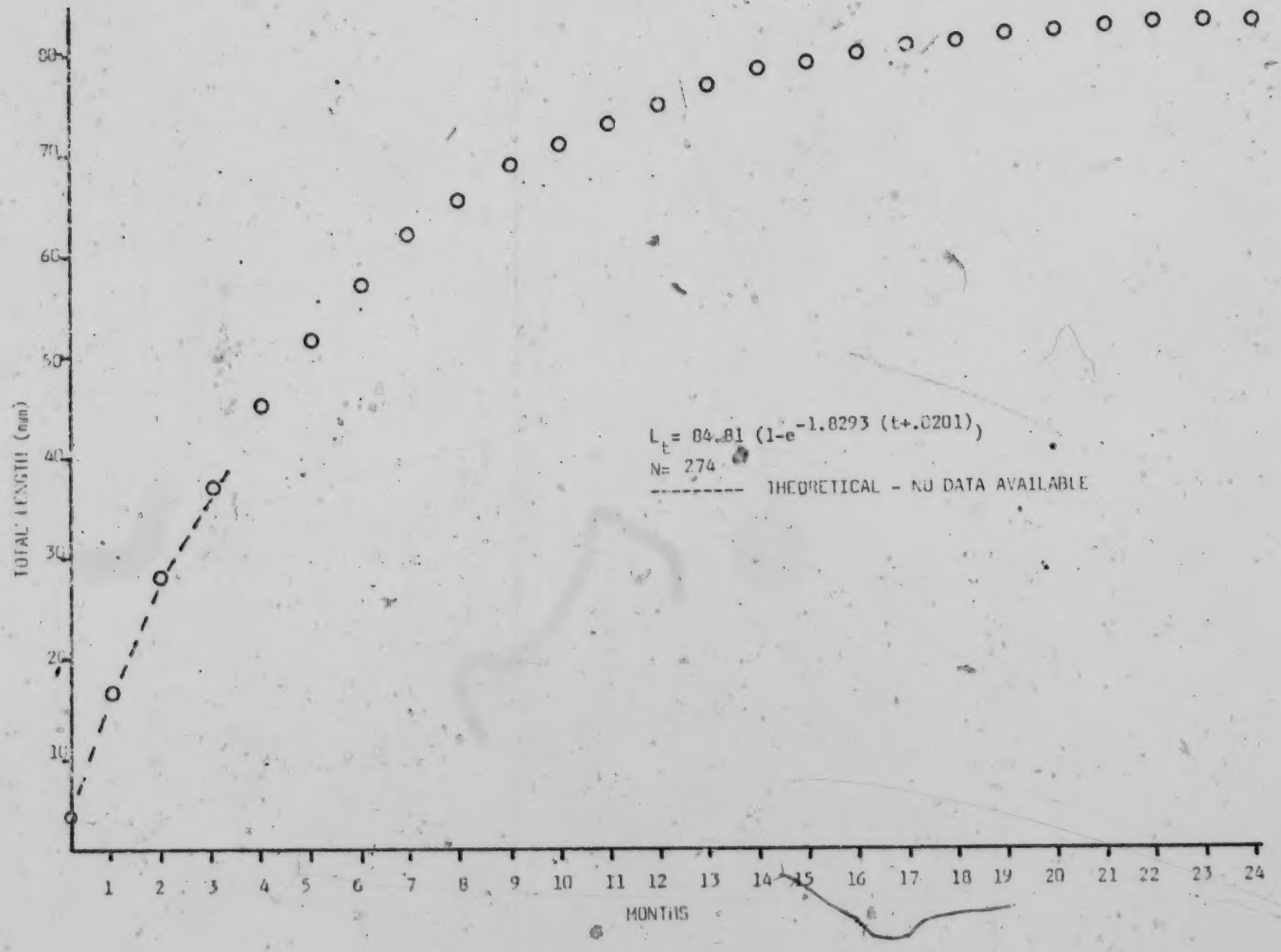

TOTAL LENGTH (mm)
80
70
60
50
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
MONTHS
$L_t = 84.81\ (1-e^{-1.8293\ (t+.0201)})$
N= 274
THEORETICAL - NO DATA AVAILABLE

This phenomenon probably occurs because there is little seasonal fluctuation which affects growth in temperate species. In addition, this characteristic high growth pattern rapidly decreases in adult fish. Presumably, this occurrence is due to some function of reproductive activity which is spread throughout the year in tropical reef fish species.

Length-Weight Relationship

The functional relationship between length and weight was calculated for *Ophioblennius atlanticus*. Ninety-one males and 134 females were used to estimate the length-weight relationship which is described by the following expression:

$$W = aL^b \text{ (Ricker 1975)}$$

or

$$\log W = \log a + b (\log L)$$

where: W = Weight (grams)

L = Total length (mm)

a,b = Constants .

The regression of log weight on log length was calculated. A geometric mean regression was used to estimate this relationship (Ricker 1975).

For 134 adult females the best fit line is estimated to be:

$$W = 3.2 \times 10^{-6} L^{3.3}$$

$$r = .97 .$$

For 91 adult males the best fit line is determined to be:

$$W = 1.12 \times 10^{-5} L^{2.98} .$$

An analysis of covariance was performed on a subsample of 25 males and 25 females in order to ascertain if the length-weight relationship for males was significantly different from that of females. No significant difference ($P > .05$) was noticed. Therefore the male and female data were pooled. The equation for the best fit line is:

$$W = 3.5 \times 10^{-6} L^{3.27} \quad \text{(Fig. 9-7)}$$

$$N = 225$$

$$r = .95 .$$

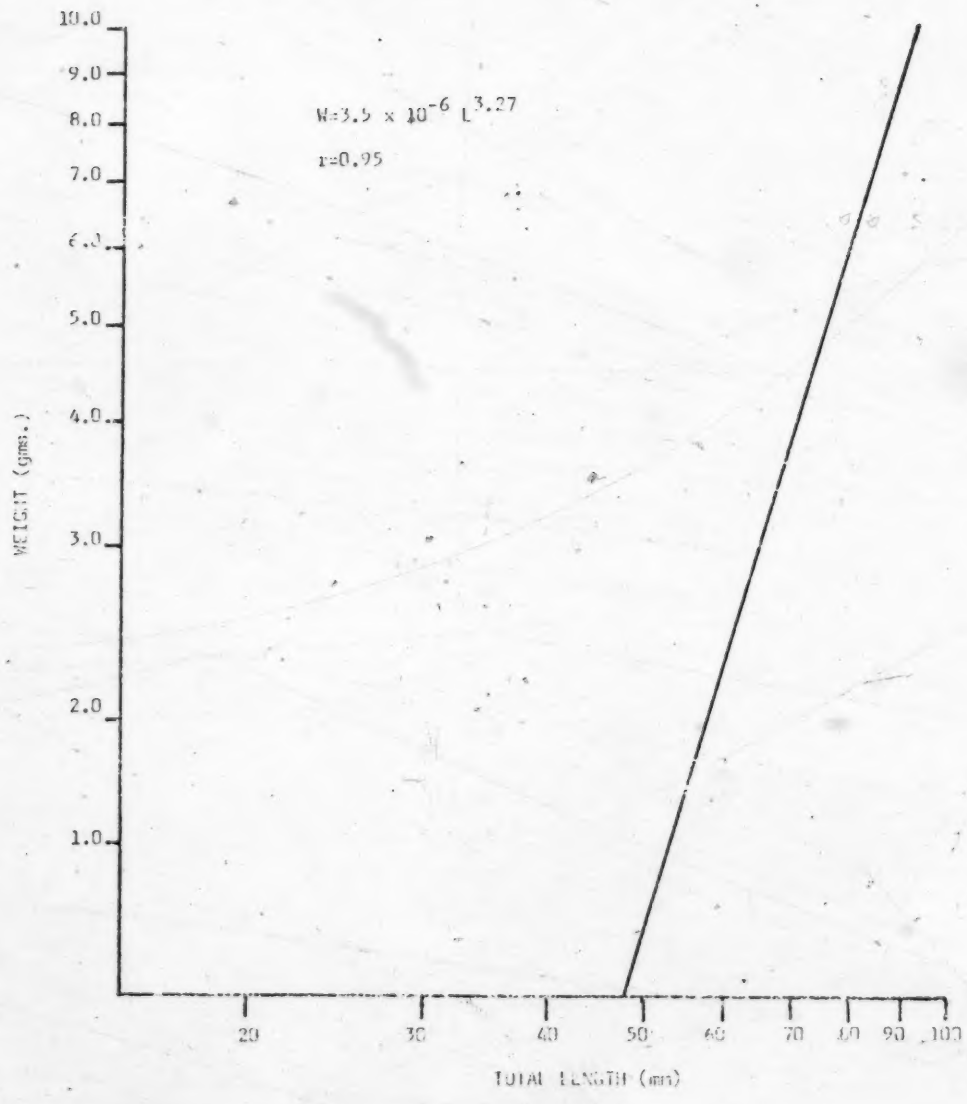
The data were again pooled for equal subsamples of 67 males and 67 females. The equation for the best fit line is:

$$W = 5.5 \times 10^{-6} L^{3.16}$$

$$r = .96 .$$

These results indicate that beyond metamorphosis growth is isometric for both sexes with respect to length-weight.

LEAF 113 OMITTED IN PAGE NUMBERING


W=3.5 x 10^-6 L^3.27
r=0.95
WEIGHT (gms.)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
20
30
40
50
60
70
80
90
100
TOTAL LENGTH (mm)

CHAPTER X

TERRITORY REPLACEMENT EXPERIMENTS

Redlip blennies hold permanent territories throughout their post-metamorphic life. A dependence on visual acuity and topographical memory by Redlip blennies in maintaining territorial boundaries is suggested by Nursall (1977a). Various authors (Rasa 1969, Hobson 1972, Myrberg and Thresher 1974) have reported on the importance of vision and topographical memory in coral reef fishes.

A field investigation was performed during July and August 1976 to test the strength of both topographical memory and also territoriality in Redlip blennies. The territories of 29 blennies were mapped according to the method used by Nursall (1977a). These blennies were then removed from their territories for periods of 30 minutes to 24 hours. The ability of a resident (a resident is recognized by its presence on its previously defined territory — Nursall 1977a) to recognize the exact limits of the territory after removal for time t, was taken as a measure of the keenness of the topographical memory. The amount of time required by a resident to regain complete control from a transgressor (a Redlip blenny from a contiguous territory which has moved across a common boundary into the territory of its neighbor — Nursall 1977a) after removal from its territory for time t, was taken as an index of the strength of territoriality. Exercise of complete control by a resident over a territory is established when the resident has both forced the retreat of all transgressors and

also completed boundary patrol. The blennies were removed from marked territories through the use of rotenone. A fish quickly placed in water without rotenone will recover rapidly and be unimpaired. After removal, a blenny was placed in a perforated plastic bag which was kept in a small holding container, attached to the substrate by means of a nylon rope. One minute before replacement, the plastic bag containing the blenny was removed from the holding container. The total length and sex of the fish were recorded at this time. The fish was subsequently taken to the marked territory and released over the middle of the territory.

The activities of the blenny following replacement were recorded. A control, consisting of a mapped territory in which the resident was not removed, was used for each set of experiments. After the resident had regained control of its territory, I would observe the general behavior pattern exhibited by the resident and compare qualitatively that pattern to the general behavior pattern exhibited by the control individual. I only looked for three gross behavior differences: extra-territoriality, agonistic behavior, and abnormal boundary patrol. In no case where the resident had regained complete territorial control were there any of these behavior differences.

The results of these experiments are summarized in Table 10-1.

Results

Five males (50-80 mm) and six females (50-76 mm) A1-11, were removed from their territories for a period of 30 minutes. When replaced, all individuals exhibited a mottled color pattern

TABLE 10-1. Summary of results of territory experiments: removal and replacement of resident Redlip blennies.

Code	t - Time Resident Is Out of Territory (minutes)	Sex	Total Length (mm)	Number of Transgressors	Time Required for Resident to Regain Territory (minutes)	Comments
A1	30	F	63	0	5	
A2	30	M	63	0	5	
A3	30	M	50	0	10	
A4	30	F	50	0	10	
A5	30	F	58	0	5	
A6	30	M	71	0	5	
A7	30	M	80	0	5	
A8	30	F	55	0	10	
A9	30	F	76	0	5	
A10	30	F	67	0	5	
A11	30	M	66	0	5	
B1	60	F	88	1	5	
B2	60	F	67	2	15	
B3	75	M	88	1	15	
C1	150	F	86	1	15	
C2	180	F	87	3	8	
C3	210	F	87	3	15	
D1	300	F	82	2	60	
D2	300	M	67	2	10	*
D3	420	F	84	1	70	
D4	540	M	82	1	15	*
D5	660	F	84	3	90	
E1	1440	M	86	3	-	**
E2	1440	M	82	1	-	
E3	1440	M	78	3	-	
E4	1470	F	84	2	-	
E5	1470	F	79	4	-	
E6	1440	F	81	2	-	**
E7	1440	M	90	1	-	

*Nest guard.
**Resident holds on to a small area at territorial boundary.

which is interpreted to be a nervous and excited state of behavior (Nursall 1977a). All eleven individuals immediately entered a small crevice within their territories. Within 30-60 seconds after replacement the individuals would lose their mottled pattern, emerge from the crevice, and patrol the exact limits of the territories. No replaced blenny traveled outside the territorial boundaries. Neighbors did not encroach upon the territory of the resident during its absence in these trials. The mean time after replacement for these eleven blennies to complete a patrol of their territories and to exhibit normal behavior was $\overline{X}$ = 6.36, Sx = 0.7 minutes.

Two females (67-88 mm) and one male (88 mm) B1-3, were removed from their territories for a period of 60-75 minutes. Twenty minutes after removal of the residents, there was increased feeding activity by neighbors at the boundaries of the vacated territories. Transgressors appeared X = 43 minutes after the resident had been removed. The number of transgressors varied from 1-2, and these transgressors were of the same size category as the residents. When replaced, the residents exhibited a mottled pattern and would enter a small crevice within the territory. Thirty seconds after replacement, the residents emerged from the crevice and patrolled the territorial limits. No resident traveled outside the territorial boundaries. The resident, encountering a transgressor, would immediately attempt to chase the transgressor from the territory. If the transgressor returned after being chased, or if the transgressor did not leave the territory, the resident would perform varied agonistic activities. These activities include: fluttering, lying across, and finally nipping. These

activities are defined by Nursall (1977a). When the resident had succeeded in dispelling all transgressors from the territory, it would proceed to its favored resting spot. The mean time for these three blennies to regain complete control of their territories was $\bar{X}$ = 11.8, Sx = 3.3 minutes.

Three females (86-87 mm) C1-3, were removed from their territories for a period of 150-210 minutes. Transgressors were seen within the vacated territories $\bar{X}$ = 60, Sx = 5.7 minutes after the residents had been removed. The number of transgressors within a vacated territory varied between one and three. When replaced, the residents exhibited a mottled pattern. Two residents entered crevices within their former territories. The third resident traveled outside the territory and entered a crevice. All three residents emerged from the crevices within 30-60 seconds and then patrolled the boundaries of their territories. The individual which entered a crevice outside its former territory had no problem locating and defining the limits of its former territory. The residents, encountering a transgressor, would attempt to chase that transgressor from the territory. The residents would perform a repertoire of agonistic activities towards one transgressor until that transgressor would be attacked first by a resident. The mean time for the three residents to establish control over their former territories was $\bar{X}$ = 12.67, Sx = 2.3 minutes. The level of activity exhibited by the residents was maintained at a high level for several minutes after all transgressors had been expelled. These three residents would move quickly through their territories. If a neighboring blenny approached the territorial boundary, the

residents would cross the border and chase and/or nip the neighbor. The resident would then quickly return to its own territory and continue its patrol.

Two males (67-82 mm) and three females (82-84 mm) D1-5, were removed from their territories for a period of 300-600 minutes. One to three transgressors were recorded in the vacated territories. The females had difficulty in regaining full control of their territories. The mean time required by these females to establish control over the territories was $\overline{X}$ = 73.3, Sx = 8.8 minutes over the time range considered. When replaced, all three females exhibited a mottled color pattern. Two females traveled just outside of the territory limits and entered a crevice. The third female resident stayed within the territory and did not enter a crevice. All female residents were on their territories and were patrolling the exact boundaries within 30-60 seconds after they had been replaced. The residents, encountering a transgressor, initiated a repertoire of agonistic behaviors. These behaviors included tail crossing, lying across, and nipping. The smallest individual was attacked first and only one transgressor at a time was assailed by the resident. The transgressors would quickly return to the residents' territories after they had been chased. A resident would often pursue a transgressor into another territory. After several unsuccessful attempts to force a transgressor off the territory, the resident would perform an exaggerated S-display. This display pattern consists of a slow rhythmical movement of the caudal region while the displaying fish either remains stationary or moves vertically in the water column. Wickler (Gibson

1969) concluded that for *Blennius fluviatilis* movements of high amplitude show aggression. This display has been only seen to occur in Redlip blennies that are under conditions of extreme stress. Several individuals which had been placed in the laboratory were noticed to display the exaggerated S-pattern in response to their mirror image seen in the aquarium glass. If the transgressor does not retreat after the exaggerated S-display is evoked, combat follows. The display usually did not encourage the transgressors to leave. Mouth to mouth combat followed the display. Combat ensued for only a second or two and resulted in the retreat of the transgressor. These activities continued until all transgressors were forced to vacate the territory. In one case, an increase in agonistic boundary activities by blennies in surrounding territories was noticed after three transgressors had been forced to vacate the resident's territory. This fact suggests that territory adjustment had occurred in the surrounding area during the absence of the resident.

The two males had little difficulty in regaining control of their territories. The mean time required by these two blennies to regain full control of the territories was $\overline{X} = 12.5$, $Sx = 2.5$ minutes over the period 300-540 minutes. One transgressor was present in one territory, and two transgressors were present in the other male's territory. All three transgressors were about the same size or larger than the residents. An unusual occurrence was that one transgressor in each territory had been resting in a crevice within the territory. After replacement, the residents moved out of their territories and entered a crevice. Thirty seconds later, the two residents emerged

and proceeded directly to the crevice within their territories where the transgressors were located. The two transgressors were immediately chased off the territories. They did not return. The residents returned to the crevices, and then patrolled their territories for several seconds. One resident encountered a second transgressor. The resident crossed over (lying across) the transgressor and then chased the transgressor off the territory. This transgressor did not return. After the residents had patrolled their territories, they returned to the crevices where the transgressors had been resting. Upon examination of these crevices, it was discovered that the crevices were actually nests and the residents were nest guards.

Four males (78-90 mm) and three females (79-84 mm) E1-7, were removed from their territories for a period of 1440-1470 minutes (24 hrs.). These seven blennies were tagged in order that their presence on the territory could be detected several hours after replacement. The experimental fish were taken to the laboratory and allowed to recover in an aquarium for one hour. After recovery, the individuals were marked with small colored beads sewn through the dorsal musculature below the dorsal fin. This procedure was done under (MS 222) anesthesia. The fish were then allowed to recover for an additional hour in the aquarium before they were returned to the holding container in the field. The number of transgressors during this set of experiments varied between one and four. All transgressors were about the same size as the residents. The residents exhibited a mottled color pattern when they were replaced. No resident was able to exercise full control over its territory. A short synopsis of the activity following replacement of each of these blennies (E1-7) is presented.

E-1 Male (86 mm) Observation Time - 90 minutes

The resident moved under a small rock in the territory and emerged three minutes later. The resident did recognize the territorial limits and did attempt to patrol them. Each of the three transgressors, however, exhibited a high level of aggressive behavior towards the resident. Actual mouth to mouth combat occurred. Twenty minutes after replacement, the three transgressors succeeded in confining the resident to a small area (10-15 cm) at the perimeter of the territory. The territory was visited 24 hours later. The resident was still confined to the same area. Three transgressors still inhabited the territory.

E-2 Male (82 mm) Observation Time - 60 minutes

One minute after replacement the single transgressor succeeded in evicting the resident from a crevice within the territory. The resident appeared to recognize the boundary limits and quickly moved into another crevice in the opposite corner of the territory. The transgressor pursued and again forced the resident from the crevice. The resident did not lose the mottled pattern. The resident moved to still another corner of the territory and took refuge under a small ledge which was occupied by a sea urchin, *Diadema antillarum*. The transgressor did not attempt to evict the resident from the area. The territory was visited 12 hours later. The resident was not present at this time. The transgressor inhabited the territory.

E-3 Male (78 mm) Observation Time - 20 minutes

The resident moved off the territory and took refuge under a rock which was located about one meter from the territory. The resident was now an intruder (a Redlip blenny in a foreign territory which is not concerned about boundary adjustment — Nursall 1977a) in a foreign territory and was immediately forced off that territory by its resident. The male swam further from its own territory. It exhibited the characteristic swimming pattern of an intruder (Nursall 1977a) high above the substrate. This atypical swimming pattern attracted the attention of other blennies, and these other blennies forced the intruder to keep moving. I followed the male for 6-8 meters where I finally lost sight of it.

E-4 Female (84 mm) Observation Time - 90 minutes

Five minutes after replacement, the resident emerged from a crevice within the territory. Soon after replacement, agonistic behaviors (lying across and exaggerated S-pattern) were displayed towards the resident by two transgressors which now occupied the territory. The resident was forced by these transgressors to seek refuge behind a sea urchin, *Diadema antillarum*. The transgressors made no further attempt to expel the resident. The resident inhabited the same area and still showed a mottled pattern 90 minutes after replacement. This territory was visited 12 hours later. The resident was not present at this time. The two transgressors had divided the territory between themselves.

E-5 Female (79 mm) Observation Time - 10 minutes

The resident emerged from a crevice within the territory five minutes after replacement. The resident did exhibit a mottled color pattern. One of four transgressors present quickly forced the resident off the territory. The resident now became an intruder in a neighboring territory and was forced to move. Instead of returning to its own territory, the female continued to move further away. I lost sight of this female about six meters from the territory.

E-6 Female (81 mm) Observation Time - 105 minutes

Four minutes after replacement, one of two transgressors forced the resident from a crevice within the territory. The resident quickly moved to another crevice near the boundary limit and took refuge. Nine minutes later, the same transgressor entered the crevice that the resident inhabited. The two blennies engaged in combat for one or two seconds. The resident was forced from this crevice and took refuge in still another crevice at the perimeter of the territory. The resident appeared to recognize the territorial limits because it made no attempt to cross any boundary line. During the next 30 minutes, the resident occupied this crevice while the transgressor patrolled the territory. The transgressor frequently entered the crevice which was inhabited by the resident during this period and "lay across" the resident. However, no attempt was made by the transgressor to force the resident from this crevice. This activity persisted for at least an hour. The territory was visited 24 hours later. The resident had managed to occupy safely a small area adjacent to the refuge it had occupied at

the perimeter of the territory. Two transgressors had firmly established themselves within the resident's territory.

E-7 Male (90 mm) Observation Time - 90 minutes

Five minutes after replacement, the resident emerged from under a rock which was within the territory. The resident had started to patrol the limits of the territory when the single transgressor attacked the resident. The resident quickly took refuge under the same rock that it had first hid under. The transgressor moved to a high vantage point within the territory and rested. It was noticed that the resident had received a wound near the gill area. A viper moray eel, *Enchelycore nigricans*, appeared four minutes after the conflict between the resident and the transgressor. The moray quickly slithered to the rock which was occupied by the resident and attacked the fish. However the resident fish, badly mauled, escaped and swam several meters to a coral head, *Montastrea annularis*. No blennies inhabited this area. The resident remained motionless on this head for 45-60 minutes. Ninety minutes after replacement, the resident disappeared from the coral head. A small viper moray was seen protruding its head from a crevice in the coral head near where the resident had been located. It is assumed that the resident was taken by this moray.

Discussion

Several conclusions concerning territoriality in Redlip blennies are implied by the results of this investigation. The data indicate

that Redlip blennies utilize an acute topographical memory in maintaining territorial boundaries. Twenty-seven of 29 residents which had been removed from their territories for periods up to 24 hours recognized and attempted to patrol the boundary limits within five minutes after replacement. The fact that residents which succeeded in forcing the retreat of all transgressors did not cross the boundary limits after regaining full control is supportive evidence of visual recognition of territorial limits.

The data corroborate evidence collected by Nursall (1977a) concerning the activity of territorial neighbors when confronted with a vacated territory. Nursall experimentally determined that "the removal of a resident leaves a territory unoccupied until a slow exploration and testing of vacancy has taken place by the nieghbours." He further stipulated that mature individuals and not interstitial blennies take advantage of vacated territories for the time period tested. In five experiments, Nursall estimated that transgression to a vacated territory occurred $\overline{X}$ = 52 minutes after the removal of the resident. During the present study, transgression by mature neighbors occurred $\overline{X}$ = 47.8 minutes (8 experiments) after the removal of the resident. The number of transgressors varied between one and three. No interstitial blennies were seen taking advantage of the vacated space. These results buttress the following general concepts: Nursall (1977a) defined a territory as an area where the presence or behavior of a resident excludes a conspecific. Van den Assem (1967) concluded that a territory may continue to exist for a limited period in the absence of the resident because the neighbors recognize the area as a territory of a particular resident.

The strength of territoriality in Redlip blennies is reflected in these experiments by the ability of residents to regain control of their territories from several transgressors. Redlip blennies which were moved from their territories for up to 10 hours successfully forced the retreat of all transgressors. The amount of time the resident had been absent from the territory clearly influenced the efficacy of the resident to force the retreat of the transgressors. Residents which were absent from their territories for periods up to 3.5 hours had little trouble in re-establishing complete control over their territory. Residents absent from their territories from 5-10 hours succeeded in regaining control, but had much difficulty in doing so. The size of the resident did not appear to influence the ability of the resident to re-establish control over the territory. Evidence is presented to suggest that a male nest guard may be able to re-establish quick control over the territory even though he was absent from that territory for a considerable period (5-9 hours). However, the evidence does not show that males in general hold an advantage over females in their ability to re-establish control over the territory.

Finally it is hypothesized that residents which are displaced from their territories become highly susceptible to predation and probably do not survive. Residents replaced after 24 hours in captivity did not re-establish control, and in 75% of the trials these residents disappeared within 24 hours after replacement. In addition, one displaced resident was probably taken by a moray eel. Nursall (1977a) described the atypical swimming behavior of a

displaced resident. The displaced resident (intruder) swims above the substrate and appears quite conspicuous. Blennies are poor open water swimmers, lacking an air bladder, and would be particularly susceptible to predation. In only one instance in 10 was Nursall (1977a) able to show successful establishment of a new territory by a blenny displaced from its territory for a long period.

The fact that territoriality is an important biotic control in establishing relative stability in the community of coral reef fishes has been suggested by many investigators (Sale 1971, Smith and Tyler 1972, Myrberg and Thresher 1974, Nursall 1977a, Thresher 1977). The control of distribution of blennies as Nursall suggests is through the activity of the residents in their territories. Territoriality in Redlip blennies is a multi-functional activity. The functional significance of territoriality is to provide blennies with an adequate supply of food, living space, and shelter site. In addition, territoriality in Redlip blennies is requisite for reproductive activities which include spawning, maintenance of a nest site, and defense and care of demersal eggs.

CHAPTER XI

GENERAL DISCUSSION

Coral reef fish communities are complex biological systems which exhibit high diversity within habitat type as well as between habitat type (Smith and Tyler 1972, Goldman and Talbot 1975). The maintenance of high diversity in coral reef fish communities has indeed been a focal point of discussion among investigators (Smith and Tyler 1972, Bradbury 1977, Nursall 1977b, Sale 1977, Smith 1977).

The fact that coral reef fish are habitat specialists on a broad scale (Hiatt and Strasburg 1960) is generally accepted knowledge among investigators, and such specialization may explain the complex community structure between habitat types. However, several competing hypotheses have been put forward to account for the species richness of coral reef fish within habitat type. Two major schools of thought are recognized from these competing hypotheses. One view holds that the predictability of abiotic factors in tropical environments enhances speciation which allows fine partitioning of resources by coral reef fish (Slobodkin and Sanders 1969, Smith and Tyler 1972). The antithesis of this view can best be termed the stochastic or unpredictability hypothesis (Sale and Dybdahl 1975). This view holds that within habitat type, the high diversity or complex community structure of coral reef fishes is best understood in terms of chance colonization by larvae of reef fish which utilize the same environmental resources in similar ways (guilds). Root (1967) initially defined the concept of a guild for bird species. The term "guild"

groups species which exhibit considerable overlap in their niche requirements, without alluding to taxonomic position. These competing views, however, both assume that biotic relationships rather than abiotic factors are the primary selective forces which act on fish in tropical environments. The importance of biotic factors as selective forces on coral reef fish has been discussed by Nursall (1977b). The proponents of these views are also of the opinion that the supply of living space appears to be the ultimate constraint placed on reef fish populations (Randall 1963, Smith and Tyler 1972, Sale and Dybdahl 1975).

Further understanding of the complex community structure of reef fish can best be attained by examining the life history parameters and strategies of guild members. The life history strategy of *Ophioblennius atlanticus*, a space-controlling herbivore, has been examined during this investigation. The results of this study may help to elucidate the strategies which enable coral reef fish to maintain themselves in a complex biological system.

Redlip blennies hold permanent territories and are members of the guild of territorial, demersal, herbivorous reef fish which primarily comprises the pomacentrids (damselfish). The territory functions to provide the blenny with the requisite elements needed to maintain itself: food, shelter site, and reproduction site. Although Redlip blennies defend their territories against conspecifics and interspecific competitors, blennies do share the substrate and resources within that area with guild members (e.g. *Eupomacentrus dorsopunicans-diencaeus* and *Microspathodon chrysurus*). Nursall (1977b)

describes this space-sharing phenomenon as a vertical or stacked utilization of the substratum by several guild-related species. For example, the territories of *Microspathodon chrysurus* and *E. dorsopunicans-diencaeus* are larger than that of the blenny; however, the territories of these fish are superimposed on the territory of the blenny. Precise resource partitioning by these guild members is not likely because there is considerable overlap in the use of space by these species. Aggressive interactions do not frequently occur between the species. Individuals (*M. chrysurus* and *E. dorsopunicans-diencaeus*) have been seen foraging within the territory of and near the nest of a breeding male without any interference by that blenny.

In addition, these guild members primarily utilize algae as a food source (Randall 1967). Based on the data obtained by Randall (1967), it is estimated that blennies ingest 17 species of algae and that 76.5% of the algal types utilized by the Redlip blenny are also utilized by either the Dusky damselfish[2] or by the Yellowtail damselfish. Microhabitat partitioning of food resources by these guild members does not appear to have taken place.

The results of this investigation indicate that Redlip blennies reproduce throughout the year, although there appears to be a major reproductive peak in which the majority of the population is breeding. Numerous pelagic larvae are produced during each month. Reproduction is correlated with the lunar cycle. Large unmetamorphosed pelagic larvae are recruited into the population about two to three months after hatching. Recruitment occurs throughout the year, although a

seasonal peak is recognized (early to mid-summer). It is hypothesized that unmetamorphosed pelagic larvae may be found throughout the year over deep water off the west coast of Barbados. Retention mechanisms (Emery 1972, Powles 1975) exist along the west coast of Barbados. It is hypothesized that blenny larvae are retained and are subsequently returned by these mechanisms to the inshore shallow areas where settling and metamorphosis occur. These pelagic larvae possibly enter the adult habitat and undergo metamorphosis within the substratum. After metamorphosis, they appear on the reef as juveniles and form interstitial territories (Nursall 1977a) between the territories of the adults. Redlip blennies exhibit very high growth rates during the first year of development, and it is suggested that as the young fish grows it will enlarge its territory at the expense of neighboring adults. This characteristic high growth pattern rapidly decreases at the end of the first year. Presumably, this occurrence is linked to the onset of sexual maturity and is due to some function of reproductive activity which is spread throughout the year. Redlip blennies carry out their life-sustaining processes within their territories. Non-reproductive extra-territoriality is not prevalent. Evidence is presented to suggest that resident Redlip blennies which are displaced from their territories become highly susceptible to predation and probably do not survive.

Implicit in the predictability hypothesis (Slobodkin and Sanders 1969) is the belief that tropical communities are made up of species which have evolved microhabitat specializations (narrow niche), and these species are at a distinct selective advantage within their

favored habitats. Sale (1977) noted that if the maintenance of high diversity within habitat type is explicable by the predictability hypothesis, then it must be assumed that guild-related members are both microhabitat specialists with respect to limiting resources (space and food), and also that they exhibit low overlap with respect to these limiting resources. Assuming that *O. atlanticus*, *E. dorsopunicans-diencaeus*, and *M. chrysurus* are guild-related species, then it is observed that clear partitioning with respect to living space and food resources does not occur. Although Redlip blennies prefer a solid substrate consisting of mixed live coral and eroded coral rock (Nursall 1977a), some individuals have been noticed to maintain territories on live coral, and one individual was seen living on the underside of a diving raft. Individuals prefer shallow water (0.1-3.0 m), but occasionally are observed living in deeper water (10-15 m; Collette and Talbot 1972; Ruth Dubin, personal communication). Redlip blennies do exhibit some variability in the type and location of space utilized. Redlip blennies do not appear to be microhabitat specialists which finely partition the limiting resources of space and food.

The food habits of Caribbean reef fish have been examined by Randall (1967). Nursall (1977b), using Randall's data, examined the utilization of algae by 23 selected species of coral reef fishes. He observed that more than 62% of the 212 algal forms recorded are used in common by these reef fish, and more than 25% are utilized by more than five species of reef fish. Hiatt and Strasburg (1960) also noted that differences between the foods of co-existing species are

usually minor. Although food specialists are recognized in a broad sense (Hiatt and Strasburg 1960), current data suggest that strict partitioning of food by guild members does not generally occur.

Although space is believed to be the ultimate constraint placed on reef fish populations (Smith and Tyler 1972, Russell *et al.* 1974, Sale and Dybdahl 1975, Nursall 1977b), there is little evidence to suggest that within habitats the utilization of living space by reef species is exclusive. The most convincing evidence for this argument is the fact that when coral reef fish are artificially removed from a section of the reef and the community is allowed to re-establish itself, then the new community structure (species composition and abundance) will differ from the original. This has been well demonstrated by Smith and Tyler (1975) in the Caribbean. Concomitantly, identical artificial reef structures which are situated in a particular area of the reef will not exhibit the same community structure after colonization (Russell *et al.* 1974, Sale and Dybdahl 1975). In addition, Sale (1975) examined the use of space by a guild of territorial pomacentrid reef fish. He concluded both that members of this guild have identical space requirements and that co-existence can be explained by the unpredictability hypothesis.

The unpredictability hypothesis (Sale and Dybdahl 1975) holds that space for colonization is the ultimate constraint placed on reef fish populations. Although the tropical environment is relatively constant, reef fish are short-lived sedentary animals and will be most affected by small-scale changes. Living space becomes available on the reef unpredictably in time and in space through predation and

mortality of individuals and by the physical degradation of the reef structure. The maintenance of high diversity within habitat type appears to be a response by reef fish to the unpredictability of living space and is the result of strategies employed by species. In order to adapt to the unpredictability of colonizing space, reef fish are forced to produce numerous pelagic larvae. Guild members produce non-specialized larvae which compete for suitable living space. Sale (1977) views this unique competition between guild members as a "lottery for living space in which the larvae are tickets and the first arrival at a vacant site wins that site. The lottery operates within habitats and at the level of the individual fish." Coral reef fishes do exhibit specializations on a broad scale (Hiatt and Strasburg 1960); therefore, the unpredictability hypothesis accounts for the maintenance of diversity within habitat types only. Colonization by guild members is essentially a stochastic process. The acquisition of space by a larva is not dependent on the size of the population of that species in that area, since the pool of available larvae in an area may emanate from various regions. Finally, once a larva has established itself in a suitable area, it should remain there (territoriality) for the remainder of its life span.

The strategy employed by the Redlip blenny supports the unpredictability hypothesis. Redlip blennies produce large numbers of pelagic larvae which are widely dispersed in space and in time. In fact, by linking breeding activity with the lunar cycle, Redlip blennies possess a mechanism which insures the year-round production of pelagic larvae. Redlip blenny larvae settle at a relatively large size

(35-40 mm) and metamorphosis and transformation probably occur within a crevice between territories of the adults. This behavior improves the chance of "winning" the lottery for living space because the "ticket holder" (post-larva) has an advantage by already having a foothold in the area. After metamorphosis, juveniles exhibit a high growth rate which enables them to expand their living space, form a permanent adult territory, reach reproductive maturity, and enter the "lottery" at an early age. Redlip blennies hold permanent territories and are not easily displaced from these areas by conspecifics or by guild members, because in territorial animals a considerable advantage in any encounter accrues to the resident (Hinde 1956). Nursall (1977a) determined that Redlip blennies patrol their territories and he estimated that an individual will have patrolled most of its territory within 30-60 minutes. He also concluded that blennies patrol their territories with an irregular pattern and periodicity. Territoriality with an active border patrol may also increase the possibilities of gaining more living space. An example is visualized in which three residents have territories which border on space occupied by a fourth individual of the same species. These residents patrol their own territories and approach the occupied space irregularly. When the occupied space becomes vacated through the mortality of its resident, the first resident to approach the space has the advantage in the eventual occupation of this vacated territory, although in competition for that space, size of competitors may ultimately have an effect (Nursall 1977a).

Although it was not the aim of this study to define the social relationship between *O. atlanticus*, *E. dorsopunicans-diencaeus*, and *M. chrysurus*, evidence from this investigation and from data collected by Nursall (1977a,b) indicates that there is little overlap in the utilization of space and food resources between these guild members.

The conclusion is that Redlip blennies are not precise habitat specialists, and that they are adapting to the unpredictability of living space in their environment. The life strategy of Redlip blennies is best illustrated by the unpredictability hypothesis (Sale and Dybdahl 1975), which may also explain the maintenance of within-habitat diversity of coral reef fish.

FOOTNOTES

[1]A revision of the Dusky damselfish (*Eupomacentrus fuscus-dorsopunicans* complex) was made by Greenfield and Woods (1974). These authors divided the Dusky damselfish into three species: *E. fuscus*, *E. dorsopunicans*, and *E. diencaeus*. Greenfield and Woods noted that the distribution of *E. fuscus* is limited to the area off Brazil and that *E. dorsopunicans* and *E. diencaeus* appear to replace it from Trinidad northward. It has not been clearly determined if the Dusky damselfish on the south fringing reef off the Bellairs Institute is *E. diencaeus* or *E. dorsopunicans*. Therefore, I shall use the term *Eupomacentrus dorsopunicans-diencaeus* when referring to the Dusky damselfish on the south fringing reef off the Bellairs Institute.

[2]Randall (1967) refers to the Dusky damselfish as *Eupomacentrus fuscus*. The distribution of *E. fuscus* is restricted to the Brazil coast (Greenfield and Woods 1974), and therefore the species that Randall examined must be either *E. dorsopunicans* or *E. diencaeus*. Randall refers to *E. fuscus* as a "drab shallow-water species of coral reefs and reef-sand areas." "It feeds primarily on sessile organisms, especially algae." These phrases describe the ecological requirements of the Dusky damselfish which inhabits the south fringing reef off the Bellairs Institute (Luckhurst 1972). Therefore, the food data presented by Randall (1967) for the Dusky damselfish were used to estimate overlap of food resources between *O. atlanticus*, *E. dorsopunicans-diencaeus*, and *M. chrysurus*.

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APPENDICES

Appendix 1. - The lengths (mm TL) and weights (grams) of Redlip blennies which were used to estimate the weight:length frequency distribution. The data are divided by sex and into two-month intervals. Redlip blennies were obtained by two methods. Individuals were speared at ramdom along a 40 m and a 100 m transect line. Individuals were also taken by rotenoning small patch reefs and collecting all blennies from the patch reefs.

Males		Females	
Length (TL mm)	Weight (grams)	Length (TL mm)	Weight (grams)
	June-July		
55.0	1.7	55.5	1.6
55.9	1.8	58.8	2.1
69.0	3.6	67.5	3.5
71.5	3.4	69.0	3.2
72.5	4.2	69.4	3.4
76.0	4.5	70.0	3.7
76.9	4.8	70.4	3.8
80.5	7.6	70.5	5.3
81.5	6.4	76.7	4.8
83.0	6.6	78.2	5.7
84.0	5.0	78.5	6.2
86.2	6.7	81.5	5.3
		81.5	5.6
		81.8	7.1
		83.1	8.4
		85.8	8.9
		89.5	8.6
		89.5	8.8
	August-September		
40.0	0.4	40.4	0.6
46.2	0.9	42.1	0.8
47.9	0.9	53.8	1.5
69.3	3.6	61.1	2.7
69.5	3.2	64.6	3.0
72.9	4.0	65.6	3.7
73.6	3.7	67.6	3.5
74.5	4.1	71.2	3.6
74.6	4.0	71.2	3.8
75.9	3.9	71.3	4.4
76.0	5.2	71.9	4.5
76.4	5.2	72.4	4.8
76.9	4.8	72.6	4.7
77.3	4.7	73.4	4.1
77.8	4.5	74.3	4.3
77.9	4.5	74.6	4.1

Appendix 1. - Continued

Males		Females	
Length (TL mm)	Weight (grams)	Length (TL mm)	Weight (grams)
		August-September	
78.3	5.0	74.6	4.5
79.9	5.7	75.2	5.8
80.6	4.9	76.0	4.3
80.7	5.2	76.0	5.6
81.5	6.5	76.1	4.7
81.7	5.4	76.4	5.2
81.8	5.9	76.7	4.8
82.3	6.5	76.7	5.1
83.6	6.8	77.0	6.3
84.8	5.9	77.2	6.2
85.8	6.2	78.0	5.2
85.9	5.4	78.2	5.7
86.5	6.4	78.3	5.9
87.0	6.1	78.4	6.1
87.0	6.6	78.6	5.7
87.3	7.1	78.9	6.6
88.4	6.4	79.3	5.8
		79.6	6.4
		80.5	6.9
		81.1	7.1
		81.3	6.9
		83.5	7.1
		85.0	7.6
		85.5	8.4
		90.8	7.9
		October-November	
42.0	0.8	47.5	1.1
43.5	0.9	48.2	1.0
44.4	0.9	50.8	1.3
48.1	1.1	52.8	1.7
48.2	1.1	53.8	1.5
49.8	1.3	55.3	1.7
49.8	1.3	56.0	1.7
50.0	1.2	57.2	2.1
50.8	1.5	61.7	2.3
51.0	1.4	62.6	2.6
51.3	1.4	66.9	2.8
51.9	1.4	67.4	3.5
52.9	1.7	72.3	4.6
53.2	1.6	73.6	4.5
53.2	1.5	74.2	4.3
56.4	1.7	74.6	4.1

Appendix 1. - Continued

Males		Females	
Length (TL mm)	Weight (grams)	Length (TL mm)	Weight (grams)
		October-November	
61.5	2.5	75.0	4.8
62.1	2.5	75.4	5.7
64.0	2.9	76.1	4.7
65.8	2.5	76.3	6.5
66.4	3.2	76.8	4.8
73.4	4.1	78.1	6.2
75.5	4.3	78.4	6.1
76.0	5.2	79.2	6.3
77.9	4.8	79.3	5.8
78.5	4.9	80.0	6.6
78.6	5.0	80.1	6.6
79.8	5.3	81.5	5.3
80.0	5.0	82.3	6.7
81.0	5.1	82.8	6.3
81.1	5.6	82.9	8.1
81.8	5.9	83.0	7.3
84.4	6.6	83.8	7.3
84.9	6.5	84.6	7.2
85.3	6.5	85.5	8.4
85.4	6.5	85.9	7.2
86.0	6.6	85.9	7.6
87.0	7.7	87.6	8.3
87.6	6.3	88.2	8.5
		88.5	8.9
		92.8	11.1
		February-March	
55.9	1.8	56.7	2.5
62.0	2.9	61.0	3.3
62.4	3.4	61.9	2.8
62.6	2.8	62.0	2.8
63.4	3.1	62.5	2.9
69.5	3.2	63.8	2.7
74.4	4.5	63.9	3.2
76.7	4.9	64.1	3.2
77.5	5.9	67.1	4.8
79.9	5.7	67.7	3.5
80.3	5.2	68.0	3.6
80.5	7.6	69.3	3.4
81.0	5.0	70.7	4.3
81.3	5.6	71.1	5.1
82.9	6.6	71.1	5.3
83.6	5.1	71.5	4.8

Appendix 1. - Continued

Males		Females	
Length (TL mm)	Weight (grams)	Length (TL mm)	Weight (grams)
		February-March	
90.9	8.4	71.6	4.8
91.0	7.1	72.3	4.7
95.8	8.5	73.4	5.0
		73.6	4.5
		73.7	5.8
		74.4	5.1
		74.8	6.1
		75.6	5.7
		76.2	4.9
		76.3	6.5
		76.5	4.8
		77.2	6.2
		77.8	6.1
		77.8	6.7
		78.2	5.7
		78.3	7.0
		78.4	5.2
		78.7	5.3
		78.8	5.7
		79.9	6.4
		80.0	6.6
		80.1	6.6
		80.2	6.7
		80.5	6.8
		80.5	7.0
		80.8	7.6
		81.8	7.1
		82.1	6.9
		82.2	8.6
		82.2	6.9
		82.2	8.5
		82.6	7.4
		83.0	7.3
		83.1	8.4
		83.2	6.4
		84.1	7.6
		85.2	8.3
		85.8	8.7
		85.8	8.9
		86.7	8.1
		86.8	8.0
		86.9	7.9
		87.4	8.0
		88.0	9.3
		88.3	8.0
		88.3	8.9

Appendix 1. - Continued

Males		Females	
Length (TL mm)	Weight (grams)	Length (TL mm)	Weight (grams)
		February-March	
		89.1	8.5
		89.6	9.0
		91.6	9.0
		91.9	10.4
		93.1	11.8

Appendix 2. - Raw data which was used to determine the activity patterns of eight males in reproductive condition. The numbers 1-16 refer to the 16 subdivisions of the $1m^2$ metric grid, which is illustrated below. The seven basic activities are abbreviated: N, resting within the nest; V, resting next to the nest; M, moving; Ia, intraspecific interaction; Ie, interspecific interaction; D, displaying; and F, feeding. The data represent the frequency of occurrence of a basic activity within an area during the observation period. The percent of time allocated to an activity during the observation period and the percent of time spent in a subdivision are listed.

North

1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16

Metric grid

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 1, Date 6/10/76, Time 0615, Observation Period 12 minutes																		
N		2				41											43	42
M										2			1	1			4	3.9
D						3											3	2.9
Ia													2				2	1.9
Ie																		
F																		
V						51											51	49.5
Total		2				95				2			3	1			103	
%		1.9				92.2				1.9			2.9	.97				

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 6/29/76, Time 1315, Observation Period 16 minutes																		
N															197		197	75.8
M										3	2			2	2	1	11	4.2
D																		
Ia														1			1	.4
Ie										9	3	2	1	11	3		29	11.1
F														12	9		21	8.1
V																		
Total										12	5	2	1	27	211	1	261	
%										4.6	1.9	.8	.4	10.3	81	.4		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 6/30/76, Time 0615, Observation Period 14 minutes																		
N															77		77	34.5
M									1	7			1	1	4		14	6.3
D																		
Ia									1	7	1		1		23	1	44	19.7
Ie																		
F										1							1	.45
V														3	84		87	39.0
Total									2	15	1		2	4	178	1	223	
%									.9	6.7	.45		.9	1.8	79.8	.45		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 6/30/76, Time 1321, Observation Period 15 minutes																		
N															233		233	75.4
M										3	3			11	5	1	23	7.4
D																		
Ia							3			1				2			8	2.6
Ie														2			2	.65
F										3	3			15	4		25	8.1
V														10	8		18	5.8
Total							3			7	6			40	250	1	309	
%							.97			2.3	1.9			12.9	80.9	.3		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 7/01/76, Time 0627, Observation Period 13 minutes																		
N															52		52	29.9
M									1	5	2				2	2	12	6.9
D										1	6					6	13	7.5
Ia																		
Ie											1					1	2	1.2
F															95		95	54.6
V																		
Total									1	6	9				149	9	174	
%									.57	3.5	5.2				85.6	5.2		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 7/01/76, Time 1530, Observation Period 15 minutes																		
N																		
M															206		206	69.6
D											15	14		9	3		41	13.9
Ia																		
Ie												7					7	2.4
F											2			1	1		4	1.4
V											5	9		11	3		28	9.8
											3	5			2		10	3.4
Total											25	35		21	215		296	
%											8.5	11.8		7.1	72.6			

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 2, Date 7/06/76, Time 0600, Observation Period 16 minutes																		
N															99		99	51.0
M										1	1			4	2		8	4.1
D															1		1	.51
Ia											4				2	1	7	3.6
Ie															1		1	.51
F										1							1	.51
V										6					71		77	39.7
Total										8	5			4	176	1	194	
%										4.1	2.6			2.1	90.1	.51		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 3, Date 6/30/76, Time 1411, Observation Period 13 minutes																		
N							214										214	96.8
M		2															2	.91
D																		
Ia		1															1	.45
Ie																		
F		4															4	1.8
V																		
Total		7					214										221	
%		3.2					96.8											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 3, Date 7/01/76, Time 1506, Observation Period 13 minutes																		
N						207											207	83.3
M		1	1			3	2			9	2			1			19	7.6
D											1						1	.4
Ia		2															2	.8
Ie		1				2				1							4	1.6
F			1				3			5	3			4			16	6.4
V																		
Total		4	2			212	5			15	6			5			249	
%		1.6	.8			85.1	2.0			6.0	2.4			2.0				

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 4, Date 7/08/76, Time 0608, Observation Period 16 minutes																		
N															203		203	81.2
M							2	1		5	3	3		8	6		28	11.2
D											1						1	.4
Ia							1					3		3	2		9	3.6
Ie															2		2	.8
F												1					1	.4
V															6		6	2.4
Total							3	1		5	4	7		11	219		250	
%							1.2	.4		2.0	1.6	2.8		4.4	87.6			

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 4, Date 7/11/76, Time 0602, Observation Period 20 minutes																		
N				35											230		265	78.9
M				3			5	3			4	2	1		1		19	5.7
D																		
Ia							1								45		46	13.7
Ie															1		1	.3
F																		
V				4											1		5	1.5
Total				42			6	3			4	2	1		278		336	
%				12.5			1.8	.9			1.2	.6	.3		82.7			

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 5, Date 8/06/76, Time 0700, Observation Period 15 minutes																		
N											116						116	49.6
M				11							2	19					32	13.7
D																		
Ia				41							41						82	35.0
Ie											1	3					4	1.7
F																		
V																		
Total				52							160	22					234	
%				22.2							68.9	9.4						

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 5, Date 8/07/76, Time 0624, Observation Period 7 minutes																		
N											74						74	71.8
M											2	2			3		7	6.8
D																		
Ia											3	1			1		5	4.9
Ie																		
F															1		1	.97
V											3		1		12		16	15.5
Total											82	3	1		17		103	
%											79.6	2.9	.97		16.5			

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male,6, Date 8/14/76, Time 0615, Observation Period 15 minutes																		
N										93							93	43.5
M					8			2		12		12				1	35	16.4
D																		
Ia																		
Ie							1										1	.47
F																		
V										85							85	39.7
Total					8		1	2		190		12				1	214	
%					3.7		.47	.93		88.8		5.6				.47		

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 6, Date 8/17/76, Time 0609, Observation Period 17 minutes																		
N										183							183	79.2
M									1	12	1						14	6.1
D																		
Ia									2								2	.88
Ie																		
F																		
V									2	30							32	13.9
Total									5	225	1						231	
%									2.2	97.4	.43							

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 6, Date 8/18/76, Time 0607, Observation Period 16 minutes																		
N										195							195	84.1
M									1	2				12			15	6.5
D																		
Ia																		
Ie																		
F																		
V									2	20							22	9.5
Total									3	217				12			232	
%									1.3	93.5				5.2				

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 1/31/77, Time 0625, Observation Period 12 minutes																		
N									183								183	94.3
M									8								8	4.1
D																		
Ia			1						2								3	1.6
Ie																		
F																		
V																		
Total			1						193								194	
%			.52						99.5									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 1/31/77, Time 1340, Observation Period 11 minutes																		
N									132								132	79.0
M					1				6	7				3			17	10.2
D																		
Ia																		
Ie																		
F					1				1	6				5			13	7.8
V					3				1	1							5	3.0
Total					5				140	14				8			167	
%					3.0				83.8	8.4				4.8				

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/01/77, Time 0615, Observation Period 10 minutes																		
N									145								145	95.4
M									5								5	3.3
D																		
Ia																		
Ie																		
F																		
V									2								2	1.3
Total									152								152	
%									99.9									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/01/77, Time 1340, Observation Period 12 minutes																		
N									128								128	89.5
M									3	5			2				10	7.0
D																		
Ia																		
Ie																		
F									2	1							3	2.1
V									2								2	1.4
Total									135	6			2				143	
%									94.4	4.2			1.4					

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/02/77, Time 0615, Observation Period 13 minutes																		
N									103								103	67.8
M	3				6				2	2							13	8.6
D					6				26								32	21.1
Ia									3								3	1.9
Ie	1																1	.66
F																		
V																		
Total	4				12				134	2							152	
%	2.6				7.9				88.2	1.3								

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/07/77, Time 0615, Observation Period 15 minutes																		
N									174								174	97.8
M							1										1	.56
D							1										1	.56
Ia																		
Ie																		
F																		
V									2								2	1.12
Total							2		176								178	
%							1.12		98.9									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/07/77, Time 1330, Observation Period 14.5 minutes																		
N									163								163	87.6
M					1				10	3							14	7.5
D																		
Ia																		
Ie																		
F					2				5	2							9	4.8
V																		
Total					3				178	5							186	
%					1.61				95.7	2.7								

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/14/77, Time 0615, Observation Period 12 minutes																		
N									115								115	84.6
M									2				4				6	4.4
Q																		
Ia																		
Ie																		
F																		
V													1				1	.74
									14								14	10.3
Total									131				5				136	
%									96.3				3.7					

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/16/77, Time 0615, Observation Period 12 minutes																		
N									67								67	57.8
M						2			9	2							13	11.2
D																		
Ia																		
Ie																		
F																		
V						1			37	1							39	33.6
Total						3			110	3							116	
%						2.6			94.8	2.6								

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/16/77, Time 1420, Observation Period 12.5 minutes																		
N									35								35	23.6
M						1			5				3				9	6.1
D																		
Ia																		
Ie																		
F						2			4				17				23	15.5
V									78				3				81	54.7
Total						3			122				23				148	
%						2.0			82.4				15.5					

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/28/77, Time 0615, Observation Period 11.5 minutes																		
N							5							155			160	89.9
M					1					2				6			9	5.1
D														2			2	1.1
Ia																		
Ie																		
F																		
V														7			7	3.9
Total					1		5			2				170			178	
%					.56		2.8			1.1				95.5				

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 3/02/77, Time 0615, Observation Period 8 minutes																		
N									72								72	75.0
M	1				2	1			8								12	12.5
D	1				1				9								11	11.5
Ia						1											1	1.1
Ie																		
F																		
V																		
Total	2				3	2			89								96	
%	2.1				3.1	2.1			92.7									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/18/77, Time 0615, Observation Period 13.5 minutes																		
N									73									
M					1				9								73	54.1
D	1																10	7.4
Ia																	1	.74
Ie																		
F									1								1	.74
V					13				37								50	37.0
Total	1				14				120								135	
%	.74				10.4				88.9									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/18/77, Time 1330, Observation Period 8.5 minutes																		
N																		
M					2	1			8	3							14	13.2
D																		
Ia																		
Ie									1								1	.94
F					2	3			3	2							10	9.4
V					1				80								81	76.4
Total					5	4			92	5							106	
%					4.7	3.8			86.8	4.7								

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 7, Date 2/25/77, Time 0615, Observation Period 14 minutes																		
N									127								127	78.9
M					2	1			4								7	4.4
D									3								3	1.9
IA						1											1	.62
Ie																		
F																		
V									23								23	14.3
Total					2	2			157								161	
%					1.2	1.2			97.5									

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/01/77, Time 0620, Observation Period 10.5 minutes																		
N							110										110	88.7
M							3										3	2.4
D																		
Ia																		
Ie																		
F																		
V							11										11	8.9
Total							124										124	
%							99.9											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/01/77, Time 1400, Observation Period 13 minutes																		
N							120										120	81.6
M								1			5	2					8	5.4
D																		
Ia																		
Ie																		
F												2					2	1.4
V							15				2						17	11.6
Total							135	1			7	4					147	
%							91.8	.68			4.8	2.7						

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/07/77, Time 0630, Observation Period 16 minutes																		
N							187										187	93.5
M			1				1										2	1.0
D							10										10	5.0
Ia							1										1	.5
Ie																		
F																		
V																		
Total			1				199										200	
%			.5				99.5											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/07/77, Time 1400, Observation Period 12 minutes																		
N							127										127	87.0
M		1	3														4	2.7
D																		
Ia																		
Ie																		
F		2		5			2										9	6.8
V				1			4										5	3.4
Total		3	3	6			133										146	
%		2.1	2.1	4.1			91.1											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/14/77, Time 0630, Observation Period 9 minutes																		
N																		
M						1	3										4	3.7
D																		
Ia																		
Ie																		
F																		
V						2	101										103	96.3
Total						3	104										107	
%						2.8	97.2											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/16/77, Time 0630, Observation Period 14 minutes																		
N							64											
M							8										64	38.1
D																	8	4.8
Ia																		
Ie																		
F																		
V						70	26										96	57.1
Total						70	98										168	
%						41.7	58.3											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/16/77, Time 1440, Observation Period 11 minutes																		
N																		
M		1		4		4	5										14	11.4
D																		
Ia																		
Ie																		
F		18		4			2										24	19.5
V						56	29										85	69.1
Total		19		8		60	36										123	
%		15.5		6.5		48.8	29.3											

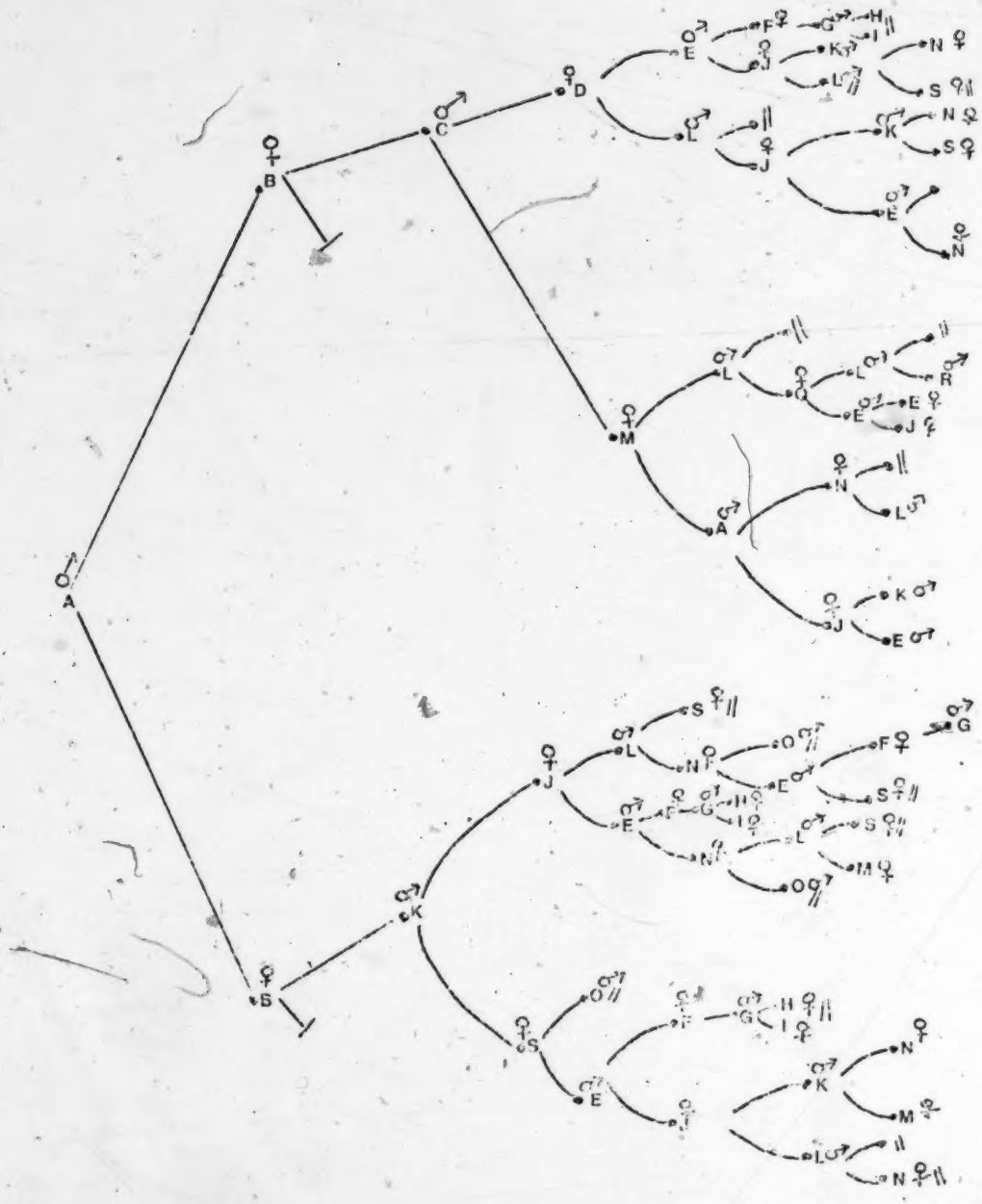
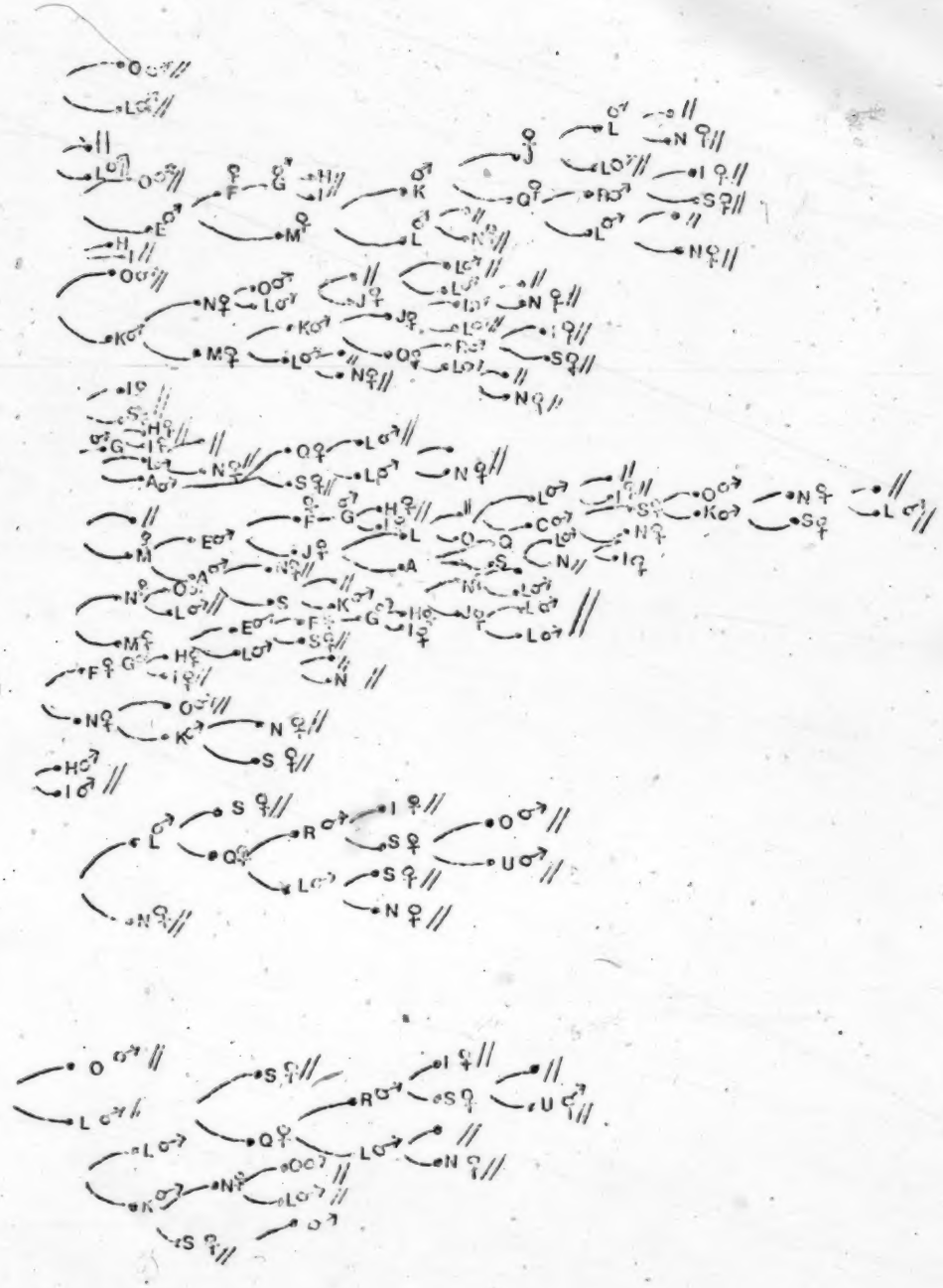
Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/18/77, Time 0630, Observation Period 10.5 minutes																		
N																		
M						1	3										4	3.2
D																		
Ia							1										1	.79
Ie																		
F																		
V						4	117										121	96.0
Total						5	121										126	
%						4.0	96.0											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/18/77, Time 1350, Observation Period 7 minutes																		
N							3										3	3.3
M					3	8	4										15	16.3
D																		
Ia																		
Ie																		
F					2	3	7										12	13.0
V						62											62	67.4
Total					5	73	14										92	
%					5.4	79.4	15.2											

Activity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	%
Male 8, Date 2/23/77, Time 0615, Observation Period 15 minutes																		
N							5							155			160	89.9
M					1					2				6			9	5.1
D														2			2	1.1
Ia																		
Ie																		
F																		
V														7			7	3.9
Total					1		5			2				170			178	
%					.56		2.8			1.1				95.5				

APPENDIX 3. - Diagram of the possible pathways of male and female behaviors that will lead either to acceptance or rejection of a female for spawning with a male in reproductive condition.

BEHAVIOR LETTER CODE	KEY TO LETTER CODE
A	MALE IN NEST
B	FEMALE APPROACHES TERRITORY OF A MALE
C	MALE COMES OUT OF NEST AND MOVES TOWARD FEMALE
D	FEMALE CONTINUES MOVING TOWARD MALE
E	MALE MOVES TO FEMALE AND PECKS HER ON THE HEAD
F	FEMALE FOLLOWS MALE TO NEST
G	MALE ENTERS NEST
H	FEMALE ENTERS NEST AFTER MALE : SPAWNING COMMENCES
I	FEMALE ENTERS NEST, MALE FOLLOWS : SPAWNING COMMENCES
J	FEMALE DISPLAYS "S" (SHOWS ABDOMEN)
K	MALE DISPLAYS "S"
L	MALE CHASES FEMALE FROM NEST AREA AND THEN HE RETURNS TO NEST
M	FEMALE APPROACHES NEST
N	FEMALE LEAVES AREA - MALE DOES NOT CHASE
O	MALE RETURNS TO NEST
Q	FEMALE ENTERS NEST
R	MALE APPROACHES NEST AND PECKS FEMALE THAT IS ALREADY IN THE NEST
S	FEMALE IS CHASED FROM AREA BY MALE
U	MALE ENTERS NEST : SPAWNING COMMENCES WITHOUT PECKING OF FEMALE BY MALE


A
B
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